IMPACTS OF MOUNTAIN PINE BEETLE (DENDROCTONUS PONDEROSAE) AND FIRE DISTURBANCES ON FOREST ECOSYSTEM CARBON DYNAMICS AND SPECIES COMPOSITION

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Impacts of Mountain Pine Beetle (*Dendroctonus Ponderosae*) and Fire Disturbances on Forest Ecosystem Carbon Dynamics and Species Composition

Thesis directed by Casey Allen.

ABSTRACT

Forests play an important role in storing and sequestering carbon, where conifer forests in particular, store more than 33% within the terrestrial carbon pool. Disturbances, such as fire and insects, impact the amount of carbon that can be stored over time in conifer forests. Stand composition and structure, which plays an important role in carbon storage over time, may be altered by these large disturbances. A mountain pine beetle (*Dendroctonus* ponderosae, MPB) epidemic has impacted lodgepole forests along the Rocky Mountains, and has potentially altered carbon storage and stand composition trajectories in the short and longterm. This research used the Forest Vegetation Simulator (FVS) to quantify the scope and magnitude of the impacts of MPB on carbon storage and stand composition in a 200 year simulation. FVS was initialized with forest inventory tree, advanced regeneration and fuels data collected in 2010 in Grand County, Colorado, where Grand County was the epicenter of the MPB outbreak in the Southern Rocky Mountains. This FVS simulation carbon and stand composition results were compared to a "control" FVS simulation, where all trees killed by

MPB were recoded as live to represent the conditions before the major mortality years of the MPB epidemic. The "MPB" simulation and "control" simulation trajectories were also compared to the trajectories of a "Fire" simulation in FVS, to compare MPB disturbance to fire disturbance.

Carbon and stand trajectories were altered between the three simulations, showing MPB has altered forest carbon storage and stand structure, which is different from how fire disturbances affect carbon and species composition. There were differences in the trajectories of carbon storage and stand composition between plots based on initial species composition as well. MPB impacts carbon storage on a relatively short temporal scale, and impacts stand composition on a longer time frame. Fire disturbance seems to affect carbon storage in lodgepole forests more drastically, and for a slightly longer time period. These results aid in management for optimal carbon storage while facing a greater potential for coarse-scale disturbances in a changing climate.

The form and content of this abstract are approved. I recommend its publication.

Approved: Casey Allen

DEDICATION

I dedicate this thesis to my beautiful daughter, Aderyn Jade Caldwell.

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I. INTRODUCTION

The thesis presented here is intended to address two main research questions. Forest disturbances can impact carbon cycling and species composition trajectories over time. First of all, it is important to be able to quantify the extent and severity of these forest disturbances. The scope and magnitude of how disturbances alter the carbon storage and species composition trajectories may vary between forest types and disturbances, which could have important implications for forest management. This thesis stands to first quantify the extent and severity of the mountain pine beetle (MPB) epidemic in eastern Grand County, Colorado. Next, the differences in carbon and species composition trajectories over time that have occurred as a result of the MPB epidemic in the study area were quantified out to 2210. Following, the carbon and species composition trajectory alterations were compared to those resulting from a simulated fire. Fires are the other common disturbance that typically affects a large expanse in the study area. The purpose is to quantify how disturbances such as mountain pine beetle and fire alter stand and carbon storage trajectories over time compared to undisturbed forests. This research also compared three categories of forest type to note differences in the trajectories for each scenario between plots, for insight at landscape and local scales. Differences in carbon storage by the stand composition in plots were also addressed. Managing for carbon sequestration and storage in

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forests could be enhanced by managing for species composition that stores more carbon.

This research is important because in order to most efficiently manage forests, it will be important to know how disturbances alter the stand and carbon storage trajectories over time. Forests, in particular, store much of the terrestrial carbon sequestered from the atmosphere. Disturbances threaten this carbon storage potential. This is an increasing threat as disturbances are projected to increase in frequency and severity during modeled warming climate scenarios. Forests will become increasingly threatened by disturbances, which could subsequently threaten carbon storage, cycling and stand dynamics in both the long and short term over multiple spatial scales.

Landscape-scale carbon flux and pool estimates reflect the dynamics of local-scale measurements, as forest stand carbon dynamics are highly variable and respond individually to differing management and disturbance regimes, as well as local-scale site characteristics and vegetation (CCSP 2007). Thus, to be able to understand the processes occurring at a landscape scale, local-scale processes must first be quantified.

This study incorporated both a field survey in Grand County, Colorado and modeled vegetation projections to quantify the impacts of an extensive mountain

pine beetle outbreak, compare the mountain pine beetle outbreak to undisturbed conditions and to a simulated fire of similar extent on stand carbon and structure. Stand carbon and species composition were tracked at the individual tree and plot level, and averaged across plots as well for a more landscape-level insight.

The basic results of this survey determined that mountain pine beetle has altered carbon and species trajectories from pre-disturbance conditions. Stand carbon, however, recovers relatively quickly, where total stand carbon storage recovers by 2040 and standing live carbon recovers to pre-disturbance storage by 2060. Stand composition trajectories have changed from pre-disturbance trajectories, from a higher percentage of the basal area being lodgepole pine to having a more mixed composition with a higher percentage of subalpine fir especially. There is some variance in carbon storage and species composition between plots by the type of overstory and understory species present in plots in 2010. Stand composition trajectories seem to rely heavily on remaining live vegetation present immediately following disturbance. The impacts of insect disturbance and how they alter stand composition and carbon trajectories differs from how fire disturbances impact them as well.

This research is organized within this thesis by a review of literature on the cycling of carbon terrestrially on a global scale, how forests and disturbances the affect forests may be impacted by climate change, carbon storage in conifer forests specifically, how disturbances impact lodgepole forests and how carbon storage,

species composition and disturbances interact in lodgepole forests. Then, the objectives of this study and uncertainties within the research are addressed. The methods are outlined by the study area, field methods and modeling, the specific model scenarios simulated, and analysis methods. The results and discussion are laid out by 2010 conditions, investigating the impacts of mountain pine beetle disturbances on carbon storage, the impacts of fire disturbance on carbon and the impacts of mountain pine beetle and fire on stand structure. Finally, the results and discussion are concluded in a summary and references are included at the end. Appendix I lists the raw plot data for two plots that were measured again in 2011 after an actual fire burned through them.

II. LITERATURE REVIEW

2.1 Terrestrial Carbon Cycling in Forests

Carbon is exchanged between and stored within the oceans, atmosphere and terrestrial carbon systems, as shown in figure 2.1 (Wigley and Schimel 2000). Carbon flux is the amount of carbon moved between pools, and carbon storage refers to the amount within a pool that is not in movement, but is steadily held. The terrestrial carbon cycle plays a significant role in the global carbon budget, as it is one of the three main reservoirs within the cycle. Forests cover about a third of earth's terrestrial land mass, fulfilling copious ecological roles (Winjum et al. 1992). One of these ecological roles is terrestrial carbon storage and sequestration within forest biomass and soils, where forests house an estimated 45-60% of the global terrestrial carbon pool (CCSP 2007). Worldwide, forests store about 2.07 x 10¹² Mg (2280 gigatons (Gt)) of carbon, and coniferous forests alone store more than 33% of terrestrial carbon (Smith et al. 1993, Kashian 2006, CCSP 2007). The main focus of this thesis will be specifically subalpine conifer forest carbon storage. Terrestrially, 36% of the land area of North America which accounts for approximately half of the carbon sink in North America is provided by forest ecosystems which offset excess atmospheric carbon inputs, such as greenhouse gas emissions (CCSP 2007,

Tallis et al. 2008). In 2003, carbon emissions in North America were about 2 billion Mg of carbon but 256 million Mg were offset by forests (Heath and Smith 2004, Birdsey et al. 2006, CCSP 2007, Pacala et al. 2007, Goward et al. 2008, Ryan et al. 2010).

In comparison, the global atmospheric carbon pool (estimated for 2003) stores about 7.05 x 10¹¹ Mg (777 Gt) of carbon as carbon dioxide, where 5.35 x 10¹¹ Mg (590 Gt) of carbon are from non-anthropogenic terrestrial sources of release, such as geologic features, fires and decomposition, and 1.69 x 10¹¹ Mg (187 Gt) are from anthropogenic contributions (Lal et al. 2000, Lal 2004, CCSP 2007). The terrestrial and atmospheric carbon pools are directly linked through forests, where forests absorb carbon dioxide and release oxygen back to the atmosphere. An imbalance between sources and sinks in the terrestrial carbon cycle may cause a subsequent increase of carbon in the atmosphere, and changes in Earth's climate (CCSP 2007).

Oceanic carbon storage is approximately 50 times greater than the atmospheric sink and cycling between the ocean and atmosphere occurs on the time scale of hundreds of years (Prentice et al. 2001). Between the ocean and atmosphere, there is about a 2 Mg/yr flux in balance overall from the atmosphere to the ocean (where 90 Mg/yr is transferred to the atmosphere to the ocean, and 92 Mg/yr is transferred from atmosphere to

ocean storage). The largest storage of carbon dioxide in the ocean is the dissolved inorganic carbon (Siegenthaler and Sarmiento 1993). The oceanic carbon sequestration capacity may be significantly reduced if the global climate warms, as it has done in modeled GCM scenarios where carbon dioxide concentrations were increased. This modeled reduction of oceanic carbon uptake occurs from increased sea-surface temperature on carbon dioxide solubility, as well as reduced vertical mixing on carbon dioxide transport from the surface to deep ocean (Friedlingstein et al. 2001). This reduction in oceanic carbon dioxide uptake increases the need for protection of terrestrial carbon sinks, which may be easier for management.

Carbon stored terrestrially could incur changes from climate change quickly. Increased atmospheric carbon dioxide could possible lead to increased vegetation and soil carbon (Prentice et al. 2001). This could be offset through increased disturbances however. This has direct implications for management, and could possibly be mitigated.

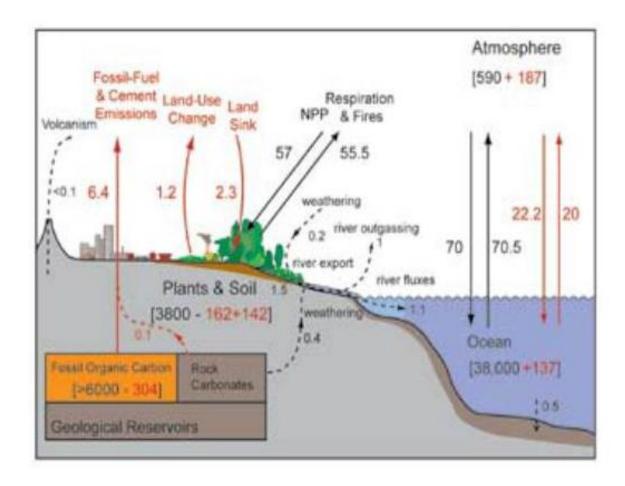


Figure 2.1 The Global Carbon Cycle (from CCSP 2007). The global carbon cycle, shown with all three primary carbon pools with fluxes. Black numbers show natural amounts and red numbers are for anthropogenic mean amounts through the 1990's. Carbon pools are in brackets, where fluxes are listed without brackets.

A primary sequestration method within the terrestrial carbon cycle occurs through vegetation, where primary productivity removes carbon dioxide from the atmosphere through photosynthesis and converts some of it to biomass (as well as respiring some back to the atmosphere), allowing for atmospheric carbon to accumulate and become stored in biomass in

what is referred to as the above-ground carbon pool (Vose 2006). Sometimes carbon input into the terrestrial carbon cycle is measured as Net Ecosystem Production (NEP), or the difference between Gross Primary Productivity (GPP) and what the plant needs to use for maintenance over time (Chapin III et al. 2002). The biomass accumulated through this carbon sequestration eventually falls and decomposes in the detrital carbon pool. And, over time, it decomposes enough to become part of the soil and humus, or below-ground carbon pool (Vose 2006). Thus, the amount of carbon stored in these pools in any ecosystem is ultimately a function of the rates of primary productivity, respiration, mortality, decomposition (Monson et al. 2002). Sources and sinks of carbon tend to determine how much carbon a particular ecosystem can store. A source of carbon outputs more carbon than it sequesters, and the opposite holds true for a carbon sink, where inputs outweigh the outputs. Typically, live vegetation is a sink for carbon. A source is an ecosystem component that decomposes and loses carbon faster than it can be sequestered. The amount of carbon stored in each component on an ecosystem can vary widely; however typically, the most amount of carbon is stored in the aboveground live vegetation and the belowground components (Chapin III et al. 2002).

Carbon sequestration is listed as an important ecosystem service, which is to say that it is a societal benefit provided by natural ecosystems.

As an ecosystem service, carbon sequestration and storage is extremely valuable to our society, and would be difficult to regain if lost (Heal 2000). In order to preserve and protect this ecosystem service, resource managers need information on how carbon is distributed and stored in specific ecosystems, as well as which carbon stores are changing and why (Joyce and Birdsey 2000, Tallis et al. 2008). Some ecosystem service models quantify carbon sequestration by splitting up the amounts sequestered in forests into four different pools: aboveground biomass, belowground biomass, soil, and dead organic matter (Tallis et al. 2008), so this research will talk about carbon storage in these four pools, generally. It is important to be able to quantify carbon stores in each pool, and important to recall that the amount of carbon stored as well as the fluxes within and between ecosystems. For example, age and type of vegetation in an ecosystem makes a difference in how much carbon can be stored in biomass. More mature forests sequester carbon in the aboveground pool more slowly than their younger counterparts (Chapin III et al. 2002, Monson et al. 2002). Due to the wide variance of carbon sequestration capacity between different ecosystems, it is important to investigate carbon storage on local scale.

2.2 Forests and Climate Change

It is uncertain how forests will respond to a changing climate. This is particularly true in the aboveground biomass pool, which may pressure changes in the other main carbon pools (CCSP 2007). Forest species ranges are projected to move northward and higher in elevation, where range expansions may impact primary ecosystem processes like succession and disturbance and subsequent changes in carbon cycling for many years into the future (Joyce and Birdsey 2000). Disturbances may increase in severity and frequency in a warming climate scenario (IPCC 2007, Bentz et al. 2010, Westerling et al. 2011). Increased drought in some areas due to climate change can make some species more susceptible to disturbance and also less productive (Dale et al. 2001). In some modeled warming climate scenarios, terrestrial ecosystems become a source of carbon dioxide, causing additional atmospheric carbon to accrue (Kurz et al. 2008, Sitch et al. 2008). There is a pressing need to understand how the potential of forests to sequester carbon may change over time in response to some of these potential impacts of climate change (Newell and Stavins 2000). Some of the uncertainties present when facing a changing climate and forest carbon cycling will be addressed later in this paper.

The negative impacts of climate change may be offset by positive changes for vegetation that could occur from increased atmospheric carbon

dioxide levels. For example, productivity of vegetation could occur. Doubling atmospheric carbon dioxide concentration, under controlled greenhouse conditions, has increased plant productivity and yield by more than 30% on average, a 37% decrease in stomatal conductance, which increases leaf temperature by 1 degree Celsius and decreases evapotranspiration, even though these percentages may vary by species (Kimball et al. 1993). However, in lodgepole forests, increased warming and carbon dioxide could have negative impacts if precipitation does not increase as well because lodgepole become moisture-stressed and their ranges shrink (Barrow and Yu 2005, Hamann and Wang 2006, Monserud 2008). The impacts of climate change on vegetation, and lodgepole in particular, are a function between the potential positive impacts on productivity and evapotranspiration compared to the potential negative impacts through disturbances and drought increases. The impacts of drought and disturbances on forests may negate the potential positive impacts of increased carbon dioxide.

2.3 Conifer Forests and Carbon Cycling

Coniferous forests cover approximately 15% of terrestrial land mass, equivalent to 10 million km² in area (Thorsell and Sigaty 1997).

Conifer forests contain 33% of all stored carbon in terrestrial ecosystems and sequester much of the carbon in western North America (Smith et al.

1993, Kashian 2006). Of the conifer forests in North America, and in the western U.S. in particular, one of the most prevalent forest types is the lodgepole pine (Pinus contorta), covering 20 million hectares (ha) of area and 6 million ha are dominated by lodgepole in the western United States (Lotan and Critchfield 2004). Within Rocky Mountain forests, the belowground pool in lodgepole forests tends to store the greatest amount of carbon (49%), followed by the above-ground vegetation (38%), detrital (12%), and understory herbaceous cover (1%) vegetation pools respectively (Birdsey 1992). Carbon storage in forested ecosystems varies with forest age and stand composition (Bradford et al. 2008). Carbon flux in a lodgepole forest has been shown to depend on climate and the spatial distribution of trees (Kueppers and Harte 2005). Although the range of carbon storage in lodgepole forests varies between sites, generally, the aboveground live carbon pool in a lodgepole-dominated forest contains around 67.9 Mg of carbon per hectare on average in the Rocky Mountain region (Birdsey 1992). The concentrated carbon in plant tissues is about 50% for overstory conifer trees, 45% for herbaceous tissues often found in a forest understory, but is highest in lipid-rich tissues from plant material, such as seeds. Carbon storage in lodgepole forests is affected by several factors, including stand density, stand age, species distribution, and is essentially a product of the balance between carbon on the forest floor and

sequestration in biomass and the carbon lost through decomposition (Kashian 2006).

Forest soils are one of the largest carbon storage components (Birdsey 1992). Carbon is incorporated into soil in the subalpine forest ecosystem from the flux of biomass from the live to the dead pool. Decomposition, a major component in the carbon cycle, is mainly carried out by fungi in lodgepole forests. Sap rot fungus is responsible for breaking down much of lodgepole litter. Fungi is responsible for much of the decomposition in subalpine forests because often soil microbes cannot survive in the acidic soils produced under lodgepole forests or cold temperatures at high elevations (Son 2010). Woody material in a forest is comprised of mainly lignin. This high lignin content combined with climatic factors and soil acidity cause decomposition in subalpine forest soils to be very slow. The biological capacity of an ecosystem to decompose organic matter is affected by organic inputs such as litterfall or excretion by organisms in the ecosystem, which subsequently exerts control on the rate of decomposition (Marschner and Rengel 2007).

Aboveground carbon storage in forest biomass is especially threatened by climate change. Small changes in the delicate balance between photosynthesis and respiration and decomposition could result in increased emissions to the atmosphere (Pregitzer and Euskirchen 2004).

2.4 Disturbances and Lodgepole Forests

Disturbances, as above-mentioned, are one factor that is expected to increase in severity and frequency under warming climate scenarios (Dale et al. 2001, IPCC 2007). Forests are periodically affected by disturbance (Roe and Amman 1970, Romme et al. 1986), or an "episodic cause of carbon loss from many ecosystems", defined by Chapin III in 2002. Immediately following a disturbance, a forest can not only discontinue sequestering carbon, but can even act as a source instead of a sink for carbon, and the time it takes for the forest to once again return to being a sink varies by forest type and stand age or disturbance history (Bradford et al. 2008, Goward et al. 2008, Kurz et al. 2008). Disturbances can alter carbon cycling dynamics considerably by causing extensive tree mortality, reducing photosynthetic capacity and potentially altering carbon flux rates between the various carbon pools (Kurz et al. 2008). Resulting changes in biomass pools and environmental conditions may alter rates of decomposition and further alter rates of other ecosystem processes, like regeneration (Dale et al. 2001). The cumulative effect is that forests can shift from being carbon sinks to carbon sources over long temporal scales (Kurz et al. 2008, Raffa et al. 2008). Some disturbance events that affect forests include fire (Romme 1982), wind blowdown (Veblen et al. 1989),

insect mortality (Roe and Amman 1970), or human management events, such as thinning and harvesting (Franklin et al. 2002).

Wildfire and insect disturbances appear to impact the largest acreage in forests in the western United States, and in the Rocky Mountain coniferous lodgepole forests mentioned above (Dale et al. 2001, USFS 2009). Fire disturbances may vary in response to a warming climate as the frequency, size and intensity of fire is directly dependent on weather and precipitation patterns, as well as forest type (Dale et al. 2001, Westerling et al. 2006). Fires are generally products of climate and available fuels (Schmoldt et al. 1999). The most extreme fire events tend to burn the most area and are controlled primarily by climate, where drought causes extreme fire seasons (Bessie and Johnson 1995). The seasonal severity rating of forest fires is modeled to increase by 10-15% depending on location by 2060, which increases forest fire activity, where fires are one of the most rapid disturbances to respond to a warming climate (Flannigan et al. 2000). Forest fires have burned increasing amounts of acreage in the last decade which can be attributed to climatic factors, such as increased seasonal temperatures and earlier snowmelt, suggesting management may not be effective if the climate continues on a warming trend (Westerling et al. 2006).

Aboveground carbon storage, such as in the aboveground live biomass and in the top layers of forest floor and downed-dead pools, could be released and turned into a carbon source if consumed by a high-intensity fire (Breshears and Allen 2002, Hurtt et al. 2002, Kashian 2006, Hurteau and North 2008, 2009). Carbon is released directly to the atmospheric carbon pool (Flannigan et al. 2000, Rapp 2004). Fire can disturb carbon storage in soils both through acceleration of nutrient cycling and changes in the top soil layer chemistry (Whelan 1995, Dale et al. 2001, Swift 2001).

Insect disturbances may be directly influenced by a warming climate, where the spread and range of insects, as well as the susceptibility of forests to insects typically increase under modeled warming climates (Dale et al. 2001, Raffa et al. 2008, Klutsch et al. 2009). Among other factors, forests become more susceptible to insects through the stress of drought in a warming climate (Amman 1977). Insects that disturb forests typically have been controlled by climatic conditions, so as climate changes, these controls are relaxed. Bark beetles, for example, may expand ranges northward, eastward, and toward higher elevations, generally (Carroll et al. 2003, Safranyik et al. 2010). This would correspond with forest species range expansions, possibly creating opportunities for greater scale disturbances, and great impacts to carbon cycling and future species succession trajectories (Joyce and Birdsey 2000).

Insect disturbances, such as the mountain pine beetle (Deondroctonus ponderosae; MPB), typically impact forests differently than other disturbances because infestation occurs in selectively largerdiameter trees (Amman 1977), potentially having different impacts to carbon storage and flux than other disturbances. MPB infests in areas where lodgepole basal area is high (Klutsch et al. 2009, Pfeifer et al. 2011). Other species of trees, as well as smaller DBH lodgepole persist in stands, where large gaps are left once trees killed by MPB fall. Some level of live biomass is maintained as compared to a stand replacing fire, which eliminates most of the live biomass over the affected area. Wildfire disturbance transfers carbon out of the ecosystem to the atmosphere and within the ecosystem in the form of ash to the forest floor, while mountain pine beetle transfers carbon to the standing dead and downed dead pools as detritus and eventually carbon is transferred to the atmosphere through decomposition on the forest floor.

MPB was the top forest mortality agent in the conterminous United States for 2009, accounting for 73% of tree mortality in the conterminous United States accounting for almost 3,500,000 hectares, as shown in figure 2.2 (USFS 2009). Historically, MPB has persisted at endemic levels in the Southern Rockies, with periodic outbreaks (Amman 1977, Baker and Veblen 1990, Raffa et al. 2008, Klutsch et al. 2009). Starting in 1996,

MPB populations have grown rapidly to epidemic levels that are unprecedented in recorded history in the Rocky Mountains (USFS 2009). The current epidemic has impacted millions of hectares (ha) of lodgepole pine (*Pinus contorta*) across North America and 777,000 ha in Colorado between 2000 and 2008 (USFS 2009). Pfeifer et al. in (2010), noted a short term change in carbon stocks and fluxes after a mountain pine beetle outbreak in an Idaho lodgepole forest, where there was immediately a maximum 83% decrease in carbon stocks and 73% in carbon fluxes (or the rate of carbon sequestration) that were recovered in 25 years or less. Pfeifer et al. (2010) surveyed 12 plots in an Idaho forest consisting primarily of lodgepole and Douglas fir (*Pseudotsuga menziesii*) and modeled the trajectory of carbon pools and fluxes after MPB killed up to 52% of trees within plots. Substantial variability of carbon stocks and fluxes resulted from the size distribution of trees within the 12 plots.

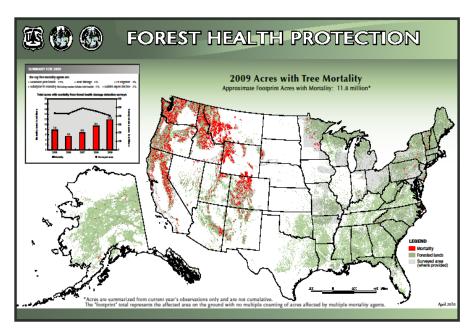


Figure 2.2 Forest Acres with Tree Mortality (From the United States Forest Service (USFS) Forest Health Damage Detection Surveys, 2009). Shows the acres of mortality, where 73% was from MPB in 2009.

Landscape-scale estimates of carbon storage change seem to depend heavily on the time since any disturbance (CCSP 2007). Both anthropogenic and natural disturbances can alter carbon cycling considerably by removing biomass and altering flux rates among biomass pools, but in spite of the recognized importance of disturbances, their potential long-term impacts on carbon cycling has not been quantified extensively and incorporated into land models that project carbon over time (Running 2008). Not only does disturbance impact short term carbon storage, it also could impact future stand trajectories and regeneration well

into the future. In turn, species shifts could cause a long-term shift in carbon storage.

Disturbances like the MPB and fire can affect species succession trajectories over long time periods. Forest species composition and tree age are important in determining how quickly carbon storage and sequestration recovers from MPB disturbances (Fahey and Knight 1986). Carbon content stored within and between species in forests can vary significantly (Chapin III et al. 2002, Lamlom and Savidge 2003, Kashian et al. 2004). Thus, efforts to quantify the long-term impacts of MPB on carbon stocks and fluxes should account for the potential changes in species composition that may occur following insect outbreaks. However, it is difficult to quantify or model future forest succession due to the many factors that must be accounted for including seed dispersal, topography of the landscape, moisture levels, competition and light availability, soil conditions and future climate scenarios.

2.5 Succession, Carbon and Disturbances in Lodgepole Forests

Fire and succession have been studied fairly extensively in lodgepole pine forests. Fires over large areas of vegetated space typically initiate successions, but these succession events are dependent on seed sources and number of advanced regeneration (Glenn-Lewin et al. 1992). Fire is important in establishing new lodgepole forests, and most of the old

growth lodgepole forests in North America were established through fire, especially in the Rockies (Lotan et al. 1985). Lodgepole sometimes produces serotinous cones, where temperatures above 45 degrees Celsius caused by fire or sometimes summer surface soil temperatures cause serotinous cones to open. This varies greatly within the Rocky Mountains, however. And lodgepole sometimes produces open cones in areas. (Lotan 1976). In the absence of fire, lodgepole can be replaced by more shade tolerant species (Lotan 1976). Management and fire suppression tend to cause fuel buildup, causing the potential for a high intensity fire that may eliminate large amounts of biomass from forest stands if a fire were to occur (Brown 1975). To recall from above, a high intensity fire is more likely in a changing climate, which could have substantial impacts on successional trajectories and carbon storage in lodgepole forests.

Impacts of insect disturbance on forest regeneration and succession have not been quantified extensively. Lodgepole typically regenerates abundantly where the mineral seedbed is adequate enough, but can be hindered by a thick organic layer that tends to inhibit seedling recruitment, where litter and fuels accumulate on the forest floor after MPB (Lotan and Perry 1983, Collins et al. 2011). Remaining canopy after MPB may inhibit lodgepole establishment, and favor the growth of more shade tolerant species, such as Engelmann spruce and Subalpine fir (Claveau et al. 2002,

Collins et al. 2011). Post-MPB lodgepole regeneration is not limited by the viable seed availability in the serotinous cones left behind (Aoki et al. 2011). Forest recovery after MPB may rely more on seedlings, saplings and residual live tree biomass, collectively known as advance regeneration, rather than new seedling recruitment, especially with the influence of a deep litter layer on the forest floor (Klutsch et al. 2009, Collins et al. 2011). Pre-epidemic forest conditions are a large determinant of MPB post-epidemic forest trajectories (Diskin et al. 2011). Modeling advance regeneration could provide greater understanding of future forest species composition and carbon storage.

Post disturbance stand species composition is dependent on time since stand initiation and severity of disturbance as well, where "secondary non-fire disturbances", such as MPB, that are high in severity, in young stands that have recently incurred fire disturbance, seem to favor lodgepole pine re-establishment (Sibold et al. 2007).

2.6 Lodgepole Pine Ecology

Lodgepole pine is shade intolerant, and grows in three different ecological roles: seral, persistent and climax (Roe and Amman 1970).

Lodgepole is able to colonize after disturbances because they have easily dispersed seeds, can grow where the canopy is open and can grow on non-ideal sites, such as nutrient-poor soils or steep slopes (Parker and Parker

1983). Persistence of lodgepole dominance in a stand is driven by topographic variables, fire frequency, seed sources, as well as an insect disturbance. Endemic MPB kills larger DBH lodgepole in 20-40 year cycles until lodgepole is eliminated from the stand (Amman 1977, Romme and Knight 1981).

Changes in the dominant canopy of forest stands where gaps are introduced drive species composition and seedling establishment after a disturbance (Klutsch et al. 2009), and consequently impacts carbon storage. Specifically in Rocky Mountain National Park, Colorado, lodgepole pine distribution is defined by elevation and moisture, and to a lesser extent, summer soil moisture and sand content, where the transition from lodgepole forests to subalpine fir forests correlated with summer soil moisture (Stohlgren and Bachand 1997). The impacts of MPB disturbance on stand trajectories in Rocky Mountain National Park vary based on preepidemic stand structure and composition, where there was high variance in future stand trajectories between overstory and understory species types present in plots before a MPB outbreak (Diskin et al. 2011).

III. OBJECTIVES AND UNCERTAINTIES

3.1 Objectives

It is possible that carbon storage potential in live biomass has been reduced due to the extensive tree mortality in the Southern Rocky Mountains as a result of an extensive MPB outbreak, and potentially impact carbon storage over longer time periods through changes in stand structure and species composition. Ecosystems encompass numerous complex interactions that define and drive carbon storage and flux, and future stand composition. Quantifying the long-term impacts of insect outbreaks can be difficult because multiple processes must be accounted for including mortality, vegetation regrowth and succession, changes in primary productivity and decomposition rates, and potential for future disturbances. One of the best ways to incorporate these multiple processes is to utilize a modeling approach. Rates of mortality, drivers of growth and regrowth, potential for future disturbances and sometimes climatic variables can all be included with the use of ecosystem models. Also, when there is no historical analogy to events, such as massive epidemic-scale outbreaks, models can be used to project the potential trajectory after such event more efficiently than from observation of past and current events alone.

The objectives of this study were to quantify the amount of time required for aboveground forest carbon storage to recover to pre-MPB outbreak levels for the actual epidemic that has occurred in a Rocky Mountain lodgepole forest, as well as to investigate species composition response to MPB disturbance in order to better understand how carbon storage will change over various temporal scales in insect-disturbed forests. Then, the carbon and species succession data corresponding to the MPB epidemic will be compared to the carbon storage change and species composition after a simulated fire, to compare the impacts of these two common natural disturbances. A combination of in-situ field data collection and vegetation simulation modeling was used to quantify carbon and stand structure in the Southern Rocky Mountains. It could possibly take a very long time for carbon storage to regain the carbon storage potential they would have had if not for the MPB due to high tree mortality, decomposition of increased litterfall from dead trees, and even potential species composition change. We compared the trajectories of vegetation growth and mortality on plots that had been impacted by MPB, where peak mortality occurred 2006-2008, to the trajectories of the same plots had there not been epidemic-level beetle activity to measure the amount of carbon and species composition response through basal area

over time to the MPB disturbance. Carbon was tracked in standing live, standing dead and downed dead pools over time.

3.2 Uncertainties and limitations

There are several uncertainties with this research that must be addressed. Only aboveground carbon is quantified, where much of the carbon in forest ecosystems is stored in the soil and root system. Lodgepole biomass is 20% belowground within the root system, so only part of the entire system is accounted for (Comeau and Kimmins 1989).

Not only is carbon storage and sequestration affected by stand density, composition and age, it is also a function of litter decomposition and fall rates (Kashian et al. 2004). This research did not address decomposition, fall rates or belowground soil processes. Also, FVS, the model used for these simulations, does not account for soil type or texture, which is important in succession and carbon storage.

This research addresses conservative estimates of stand structure trajectories but does not address future disturbances that could potentially go along with those future trajectories, such as an increase in other disturbance insects or disease, such as spruce beetle or mistletoe. It could be difficult to track disturbances with the uncertainty that occurs with climate change.

Improvements to this modeling method would be to incorporate soils and belowground processes and future disturbances for an integrated approach. Also, better, less conservative, regeneration estimates would have aided in projecting stand trajectories over time, such as utilizing better predictors from wind dispersal, mineral seed bank data and typical stand trajectories after MPB disturbance.

IV. METHODS

4.1 Field Measurements and Modeling

In order to quantify the impacts of a MPB outbreak, and further the study of disturbance impacts on carbon storage and succession in the study area, I combined field data collection with vegetation simulation modeling. Model simulations can track large amounts of carbon and species composition over time, and make projections based on current trajectories (Bazzaz 1996). This methodology was also chosen because there is no historical analogy to the current mountain pine beetle outbreak, where modeling allows me to initialize the simulations with current conditions established with field data and then quantify potential changes in forest vegetation and carbon under a series of scenarios.

4.2 Study Area

The study area was located in eastern Grand County Colorado (105° 43' 32" - 106° 0' 47" W and 39°54' 58" - 40°18' 2" N). Forests in the study area are even-aged stands of lodgepole pine (*Pinus Contorta*) with subalpine fir (*Abies Lasiocarpa*) seedlings and saplings. Average stand age is approximately 70 years. A large percentage of the study area is public land where most wildfires are suppressed. Until recently, the disturbance history of the area consisted of fires of mixed severity and periodic bark beetle outbreaks at endemic levels. Beginning in 1996, an extensive and severe MPB outbreak started in the Southern Rocky Mountains- with peak MPB mortality occurring between 2005 and 2008. The

epicenter of this outbreak was in Grand County, making it an ideal area for studying the impacts of MPB and other disturbances on forest vegetation and carbon storage.

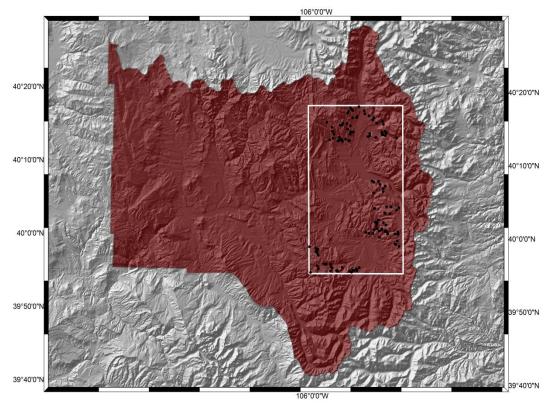


Figure 4.1 Study Area. This map shows the study area within eastern Grand County, Colorado where 119 field plots were placed in a randomly stratified sampling scheme and forest inventory data was collected.

4.3 Field methods

Field measurements were collected to characterize forest vegetation present in 2010, following the peak of MPB mortality. Plot locations were selected using stratified random sampling. The strata used included a gradient of years since peak MPB mortality derived from the Forest Health and Monitoring Aerial Surveys (1 year, 2-3 years, 4-5 years, and 5+ years), elevation (elevation quartiles), and aspect (north, south, east, west, and flat), for a total of 80 different strata. Plot locations were restricted to public lands and areas classified as Rocky Mountain Lodgepole

Pine Forest, Southern Rocky Mountain Ponderosa Pine Woodland, Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland, Rocky Mountain Subalpine Mesic-Wet Spruce-Fir Forest and Woodland, Southern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest and Woodland, or Southern Rocky Mountain Mesic Montane Mixed Conifer Forest and Woodland in the LANDFIRE existing vegetation type layer (Zhu et al. 2006, Rollins 2009). This sampling scheme was selected because it ensured that the field data captured the range of variability in biophysical gradients and MPB mortality present in the study area. 2-3 plots were placed in each stratum randomly, but revised plot locations based on accessibility; plots in potentially dangerous and inaccessible locations were manually moved within strata. Ultimately, data was collected at 119 plot locations.

A field crew measured trees, seedling and saplings as well as surface and canopy fuel loads using the Fire Effects Monitoring and Inventory Protocol: FIREMON (Lutes et al. 2006). Each plot had a fixed radius of 8 meters. Trees were defined as woody vegetation with a diameter at breast height (DBH) \geq 12 cm and total height \geq 1.4 m. Plots were overall categorized based on a primary overstory species, understory species and soil type at plot center. The tree data included a bearing distance measurement from plot center, as well as DBH, total height (measured using a Haglöf Vertex Laser), status (live or dead), number of years dead, and cause of mortality. Saplings were defined as any woody vegetation

with DBH < 12 cm and height \geq 1.4 m. Seedlings had DBH < 12 cm and height < 1.4 m Seedlings and saplings were counted within a 3.6 m radius subplot and classified according to species and diameter (saplings) or height (seedlings). Down-woody debris were measured along three transects between 5 and 25m from plot center. Data on tree and herbaceous cover were also collected along each transect at 15 m and 25 m from plot center.

4.4 Modeling methods

I initialized the Forest Vegetation Simulator (FVS) model (Stage 1973, Dixon 2003) Central Rockies Variant, with plot data from the 119 plots to simulate potential changes in vegetation composition and carbon storage as a result of the MPB outbreak. FVS is a growth and yield model, created and used by the USDA Forest Service to help manage forests across the United States. FVS is aspatial and simulates individual tree growth in stands using multiple forestry growth, diameter and height algorithms. FVS estimates changes in carbon storage over time with carbon pools split into aboveground total live, belowground live, belowground dead, standing dead, downed dead wood, forest floor and herbaceous cover. First, FVS estimates growth of trees for each cycle by diameter and height. Then, it estimates mortality based on the individual tree variables like diameter, as well as on stand variables like basal area or stand density index. Crown ratio (provided as part of the initialization dataset collected in the field), crown competition factor and total basal area, and stand density index calculations in FVS help the model

project stand trajectories over time. Mortality is primarily projected using stand density index (SDI) measurements per plot in an effort to model stand densities realistically where they do not exceed natural stand densities seen in the Central Rockies, however, background tree mortality was suppressed so as to project the trajectories of species and carbon immediately following a disturbance and not introduce new or multiple independent variables. Each growth cycle for the scenarios lasted 10 years and the output tree list from FVS reads stand and individual tree level projections for each growth cycle.

FVS was chosen over other models for several reasons. It incorporates forest growth at the tree and stand level, as compared to other models that operate over landscape scales, such as LANDIS or BIOME-BGC (White et al. 2000, Mladenoff 2004). FVS was designed to track carbon storage pools, as well as forest biological variables, like seedling and sapling growth and tree death (Crookston and Dixon 2005). It also incorporates many kinds of disturbances, and has been tested and validated specifically for the Rocky Mountain region in the Central Rockies variant that I used in this research (Dixon 2003). It focuses on aboveground carbon storage and biomass, instead of being focused specifically on belowground processes, such as CENTURY (Parton 1996).

4.5 Model Scenarios

Field measurements collected in 2010 were used to quantify the initial impacts of the MPB outbreak. Then, future carbon stocks were simulated for 200

years. Three simulations were initialized in FVS. For the first simulation, referred to as the "MPB scenario" hereafter, I parameterized FVS using field data from all 119 plots exactly as they were collected, where an average 72% of basal area was classified as 'dead' because of MPB activity. The second simulation, referred to as the "control scenario", was intended to represent near pre-outbreak conditions. In the control scenario, the input tree list was altered to reclassify all trees that had recently suffered MPB mortality to live status. For the third simulation, known as the "fire scenario", the control scenario input tree list was burned in 2010 for 72% of basal area was killed. This matched the average area killed by mountain pine beetle so as to compare carbon storage and succession trajectories between the disturbances. The simulated fire maintained default parameters for the study area in climatic variables. Each simulation was run forward to 2210.

For each of the scenarios, I used the FVS "partial regeneration" model using seedlings and saplings present in plots in 2010. Regeneration was modeled conservatively where future disturbances, factors behind regeneration (such as wind or seed dispersal), soil processes and decomposition were not taken into account. It is difficult to model these factors. Regeneration is difficult to predict because the impacts of light, moisture, climate change, soil changes and overall disturbance have differing impacts on regeneration. Soil is difficult to model because it is highly variable across spatial scales, especially at a landscape level. Also, decomposition rates are also difficult to predict. FVS simulations for both

scenarios produced annual data on the growth and attributes of individual trees, including new seedlings added each cycle, as well as plot level characteristics such as trees per hectare (TPH) and basal area (BA) per species, and carbon storage and fluxes among carbon pools. Simulation cycles were set to 10 year growth cycles and individual trees as well as plot-level summaries were given as output for each growth cycle.

This methodology to couple field data with the FVS model to track carbon storage and fluxes was used in Pfeifer et al. (2010), where FVS was initialized for 12 plots in an Idaho lodgepole forest after a MPB outbreak had occurred. They did not simulate fire, and their plots consisted of slightly different composition, nor did they track stand composition trajectories.

Collins et al. (2011) modeled species succession trajectories over time in the Southern Rocky Mountains using advanced regeneration after a MPB disturbance in lodgepole stands using gridded field data and FVS, but did not include an assessment for stand carbon.

4.6 Analysis Methods

To compare near- and long- term impacts of MPB outbreak on carbon storage and species composition, I first compared the differences in the vegetation conditions used to initialize FVS. This comparison also provided the baseline measurements of carbon storage and species composition to evaluate simulated potential changes against. Specifically, I compared total stand carbon overall as well as differences in standing live, downed dead and standing dead carbon pools between the three scenarios using Welch 2-sided t-tests assuming unequal variance. To address the research questions investigating how carbon storage changed over the years following a MPB outbreak, the MPB disturbance trajectory was compared to the control scenario. Then, to investigate differences in how fire disturbances compare to MPB disturbances, a simulated fire scenario was compared to the control scenario as well. The same approach was used to compare the baseline initial and simulated potential changes in TPH and BA by species for each scenario over time to address how species composition changed as a result of the MPB outbreak or fire.

Plots were further categorized for analysis into dominant overstory and understory combinations, modified from the method used to categorize plot types in Diskin et al. (2011), where plots were split up by 5 different forest types in order to track species trajectories based on the advanced regeneration present

before a MPB epidemic. For this research, I categorized plots based on the overall dominant overstory and understory as well, however, there were only three main types of plots. Of the 119 plots, 103 were dominated by an overstory of lodgepole pine. The other 16 plots were dominated by subalpine fir or Engelmann spruce. The plots could further be categorized by the understory level, or advanced regeneration, of trees, where there was a split between those plots that were predominately subalpine fir in the understory, and those that were predominately lodgepole pine in the understory. The majority of plots could be split into three type categories, locations illustrated in figure 4.2 and examples of each plot type in figure 4.3. The first type of plot had a stand structure with an overstory dominated by lodgepole pine, and an understory consisting of primarily subalpine fir; there were 17 plots in this category. 79 plots could be characterized by the second type, which had both an overstory and understory dominated by lodgepole pine. The third type of plot was dominated in the overstory canopy and understory by subalpine fir; there were 7 plots in this category. The rest of the plots contained aspen, Engelmann spruce or other species. There didn't seem to be any apparent pattern to the aspect, slope or elevation when compared to vegetation composition. This was possibly due to our stratified sampling design. The plots dominated in the overstory and/or understory by subalpine fir were in very specific soil texture types, where subalpine fir plots grew in sandy clay loam, clay loam and fine sandy

loam. The lodgepole plots were in these soil textures, as well as a broad spectrum of other soil texture types.

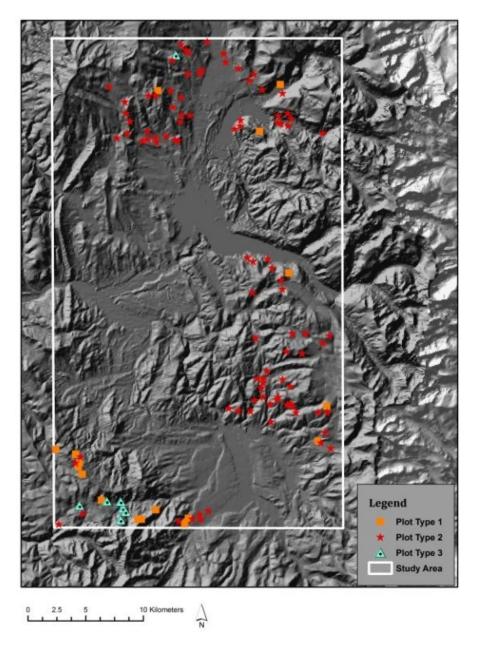


Figure 4.2.Field Plots by Dominant Composition Type. Map shows study area with spatial distribution of plots in each of the three plot species type categories.



Plot Type 1: Lodgepole Overstory, Subalpine Fir Understory 17 Plots



Plot Type 2: Lodgepole Overstory, Lodgepole Understory 79 Plots



Plot Type 3: Subalpine Fir Overstory, Subalpine Fir Understory 7 Plots

Figure 4.3 Plot Types. Photos illustrate an example of each category of plot type.

V. RESULTS

5.1 2010 Conditions

Of 6257 trees and advanced regeneration surveyed in 119 plots, 86% of trees per hectare were lodgepole pine representing 85% of the total tree basal area across plots; 74% of the total number of trees inventoried had MPB mortality (72% of total tree basal area) and 12% were healthy lodgepole (13% of total tree basal area). The MPB outbreak in our study area began in 1996, and peak mortality occurred 2006-2008, where the majority died in 2007, as shown in table 5.1. Lodgepole pines killed by MPB tended to have a larger DBH than live lodgepole pines (mean DBH was 16.2 cm for live lodgepole and 22.6 cm for dead lodgepole, p-value for 2-sided t-test of means assuming unequal variance was << 0.0001). 7% of trees in plots were subalpine fir (6% of total tree basal area) and 6% of trees were healthy subalpine fir (representing 5% of total tree basal area as well) and 1% was sick or dead subalpine fir (1% of basal area). About 4.6% of trees were Engelmann spruce (representing 5.8% of total tree basal area), with 4.2% of trees being healthy (4.7% of basal area) and 0.4% sick or dying (1.1% basal area).

Across all plots, seedlings (measured in trees per hectare (TPH)) were dominated by lodgepole pine, where TPH was 336 averaged across plots.

Subalpine Fir and Engelmann spruce were the next most common species with an average 252 and 261 TPH across plots, respectively. Saplings were dominated by

lodgepole as well, with 359 TPH on average, and subalpine fir representing an average 244 TPH and Engelmann spruce averaging 218 TPH. Lodgepole was more plentiful in the control scenario saplings, representing 370 TPH.

Table 5.1 Surveyed Lodgepole Pine Mortality. Table showing the number of lodgepole pine surveyed in 2010 in each MPB mortality category, where mortality ranged from 2004-2009.

MPB Mortality	Count of surveyed trees in 2010 field data
1 year ago: full crown of fading needles	53
2 years ago: ≥ 50% orange needles remaining	226
3 years ago: < 50% needles remaining	566
4 years ago: no needles remaining but small and large twigs present	269
5 years ago: only large twigs remaining	37
6+ years ago: both small and large twigs not remaining	14
Unknown	15
Grand Total of Trees	1180

Carbon is calculated in FVS by standard forestry procedures, where amount of carbon is half the biomass measurement (Avery and Burkhart 2002). Dry tons/hectare of biomass (where biomass is a measurement of the amount of living material calculated in FVS by the DBH and height of each tree) multiplied

by .5 for all categories except the litter and duff calculations calculates all aboveground measurements listed for carbon. It is standard to calculate litter and duff carbon by multiplying the dry biomass in these categories by .37 (Dixon 2003). These carbon estimates were part of the FVS output, and were listed for each 10-year cycle, beginning in 2010. In 2010, the average amount of total carbon per plot was 94.7 Mg/ha, but would have been 107 Mg/Ha if there was no MPB-caused mortality (p-value of .01). The standing live carbon pool averaged at 21.5 Mg/ha, but would have stored 57.2 Mg/ha had the outbreak not occurred, where pre-outbreak conditions stored 2.67 times more carbon in the standing live pool (p-value << 0.0001). Standing dead pools on average had 28.3 Mg/ha versus the 1.2 Mg/ha they would have contained without the MPB disturbance (p-value <<0.0001). In 2010, the downed dead pool averaged 19.5 Mg/ha of carbon, where it was not possible to estimate pre-outbreak downed dead wood (p-value of 0.8796).

In August 2011, two plots in the study area actually burned in a fire (plot 22 and plot 6111). Both of these plots were "type 3" plots. The plots were reexamined in September 2011. The fire resulted in every tree in each plot being transferred to the standing dead or downed dead pool, some even classified as "gone". The plot data taken for these two plots in September 2011 is given in Appendix A, where the raw plot data serves as an example of the field data collected, and as information on the fire.

5.2 Impacts of MPB on Carbon Storage

After a 200 year simulation, the total stand carbon (which includes the sum of the standing live, belowground live, belowground dead, standing dead, downed dead, herbaceous cover and forest floor measurements), was similar with 271 Mg/ha in the control scenario, and 267 Mg/ha for the MPB scenario (p-value for 2-sided t-test of means assuming unequal variance between the two datasets was 0.4). The slight, but statistically insignificant, differences were because of an increase in live biomass when MPB mortality was reclassified as live trees in the control scenario. Carbon between the simulations is listed in figures 5.1-5.4. Without additional disturbances added to the simulation throughout time and mortality turned off, total stand carbon (figure 5.1) increased steadily in both the MPB and control simulations, but was consistently greater in the control scenario than the MPB scenario. However, by 2040, total stand carbon reached 115 Mg/ha, which was not significantly different (p-value of .15) than total carbon stored in the control scenario in 2010, representing pre-outbreak conditions (107 Mg/ha).

The amount of standing live carbon was greater in the control scenario than the MPB scenario throughout the 200 year simulations (Figure 5.2). Average standing live carbon was 136.1 Mg/ha in the MPB scenario, and was 145.7 Mg/ha in the control scenario by 2210 (with a p-value of 0.0009). Standing dead carbon was higher in the MPB scenario, but not significantly when compared to the

control simulation in 2210 (Figure 5.3) with 4.3 Mg/ha and 3.7 Mg/ha respectively (p-value of 0.13). However, there was a rapid decline in standing dead biomass during the first 30 years of the MPB simulation as dead trees fell and were transferred to the downed dead carbon pool. Consequently, the downed dead carbon pool increased dramatically during the first 30 years of the MPB scenario (Figure 5.4). For the remaining years of the simulation, there were negligible differences in standing dead carbon between the two scenarios (p-value of 0 .15). Carbon in the downed dead pool increased steadily over time for both simulations, but was generally greater in the MPB scenario, with 58 Mg/ha in the control scenario and 63 Mg/ha in the MPB scenario. However, after 120 years of simulation the differences between the two scenarios were less pronounced.

5.3 Impacts of Simulated Fire Disturbance on Carbon Storage

In order to compare the impacts of MPB disturbances to fire disturbance on carbon and species composition trajectories, a fire was simulated to burn 72% of basal area (same as the average basal area affected by MPB disturbance in the plots) on the control scenario input table, to be referred to as the "fire scenario". Carbon storage and stand structure trajectories were compared between the fire scenario and the control pre-disturbance scenario, and subsequently to the MPB disturbance scenario. The fire scenario showed the lowest amount of carbon stored in all four pools of carbon, which is also shown in figure 5.1-5.4. In 2010, after the fire was simulated (in late summer for default climatic conditions for the central

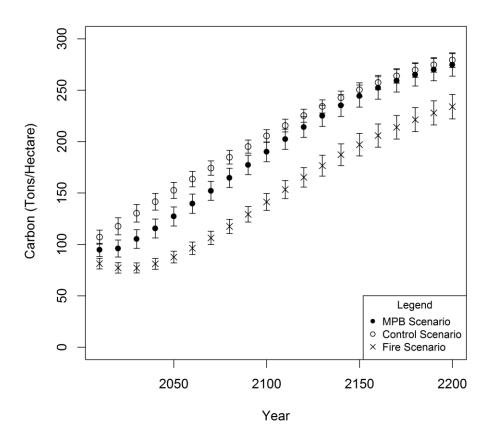
Rockies variant), the standing live carbon pool stored 79.4 Mg/ha (p-value of << 0.0001 between the fire scenario and the control scenario). The standing dead pool stored 0.52 Mg/ha (p-value of << 0.0001), downed dead stored 19.91 Mg/ ha (p-value of << 0.0001) and the total stand carbon pool stored 142.6 Mg/ha (p-value of << 0.0001).

In 2010, the simulated fire reduced standing live carbon (figure 5.2) to about 19 Mg/ha from 57.2 Mg/ha in the control (p-value of << 0.0001). Standing live carbon returned to pre-fire levels also by about 2070, to about 57 Mg/ha. Standing dead carbon (figure 5.3), however, is projected to increase from 1.2 Mg/ha in the control to about 33 Mg/ha in the fire scenario (p-value of << 0.0001). The standing dead carbon pool in the fire scenario stored almost 3 Mg/ha, and the downed dead carbon pool stored 42 Mg/ha (p-value of << 0.0001). It was not possible to project pre-fire downed dead carbon for 2010 in the fire scenario because the control scenario tree input data was burned and it was not possible to validly predict pre-disturbance downed dead wood. After the fire, however, 10.9 Mg/ha remained in the downed dead carbon pool in 2010. The average amount of carbon released from the fire from all carbon pools was 35.7 Mg/ha in 2010.

The simulated fire results (figure 5.1) for 2210 showed total stand carbon to be 228.43 Mg/Ha (p-value of << 0.0001), which was slightly lower than the total stand carbon for either the MPB or the control scenarios. Total stand carbon rebounded from around 81 Mg/ha to about 107 Mg/ha (pre-disturbance total stand

carbon) by 2070 (p-value of << 0.0001) as well, representing a return to pre-fire conditions within 60 years following fire.

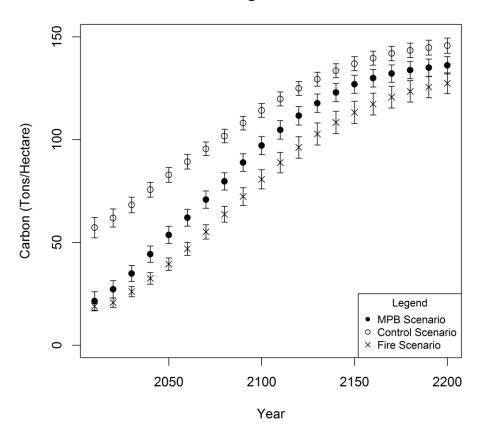
Total Stand Carbon



Year	Carbon pool	Control scenario (Mg/ha)	MPB scenario (Mg/ha)	Fire scenario (Mg/ha)
2010	Total	107 ± 6.8	97 ± 6.4	81 ± 5.3
2210	Total	271 ± 6.7	267 ± 10.2	228 ± 11.2

Figure 5.1 Total Stand Carbon. Scatter plot shows the trajectory of total stand carbon with confidence intervals, which is a compilation of all carbon pools, for each of the three scenarios: MPB, Control and Fire, where the table lists starting 2010 carbon storage and ending 2210 storage for each trajectory.

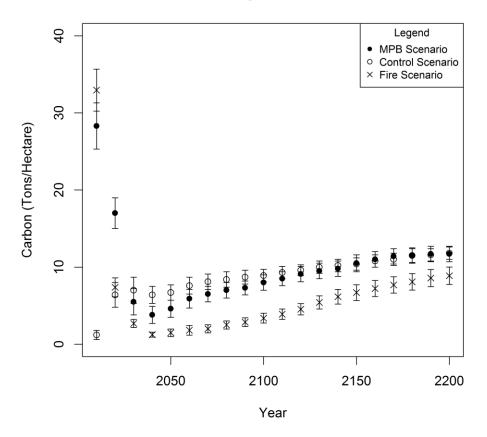
Standing Live Carbon



Year	Carbon pool	Control scenario (Mg/ha)	MPB scenario (Mg/ha)	Fire scenario (Mg/ha)
2010	Stand. Live	57.2 ± 5.0	21.5 ± 4.5	19.0 ± 2.2
2210	Stand. Live	145.7 ± 3.7	136 ± 4.2	127.4 ± 5.0

Figure 5.2 Standing Live Carbon. Scatter plot shows the trajectory of carbon in the standing live carbon pool with confidence intervals for each of the three scenarios: MPB, Control and Fire, where the table lists starting 2010 carbon storage and ending 2210 storage for each trajectory.

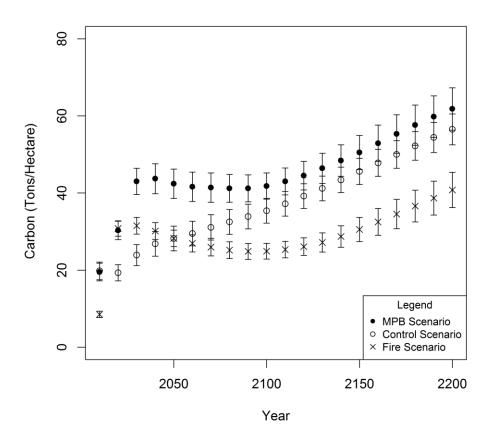
Standing Dead Carbon



Year	Carbon pool	Control scenario (Mg/ha)	MPB scenario (Mg/ha)	Fire scenario (Mg/ha)
2010	Stand. dead	1.2 ± 0.6	28.3 ± 3.0	33.0 ± 2.7
2210	Stand. Dead	3.7 ± 0.5	4.3 ± 0.5	2.9 ± 0.4

Figure 5.3 Standing Dead Carbon. Scatter plot shows the trajectory of carbon in the standing dead carbon pool with confidence intervals for each of the three scenarios: MPB, Control and Fire, where the table lists starting 2010 carbon storage and ending 2210 storage for each trajectory.

Downed Dead Carbon



Year	Carbon pool	Control scenario (Mg/ha)	MPB scenario (Mg/ha)	Fire scenario (Mg/ha)
2010	Down dead	19.5 ± 2.3	19.8 ± 2.3	4.62 ± 0.6
2210	Down dead	58.0 ± 4.1	63.0 ± 5.6	42.54 ± 4.8

Figure 5.4 Downed Dead Carbon. Scatter plot shows the trajectory of carbon in the downed dead carbon pool with confidence intervals for each of the three scenarios: MPB, Control and Fire, where the table lists starting 2010 carbon storage and ending 2210 storage for each trajectory.

5.4 Impacts of MPB on Stand Structure

Four primary species were present in stands in 2010: lodgepole pine, Engelmann spruce, subalpine fir and trembling aspen. There were a few other species, such as white fir (*Abies concolor*) and Douglas fir (*Pseudotsuga menziesii*), present in limited quantities in plots, which were grouped and referenced as "other" in figures.

In 2210, as shown in figure 5.5a, the control scenario showed a dominance of lodgepole pine in the overstory canopy, where lodgepole accounted for 58% of basal area in 2210, but subalpine fir only accounted for 19% of basal area. Engelmann spruce and aspen were subdominant species in both scenarios; however, the MPB scenario had greater proportion of aspen and spruce than in the control scenario in 2210. The MPB scenario (figure 5.5b) shows a much more even mixture of tree species in the overstory vegetation layer, where there was about 30% of basal area of each subalpine fir and lodgepole, 12.6% was Engelmann spruce, and 17.7% was aspen. For an example plot in the study area, figure 5.6 shows the FVS 2010 and 2210 results for the MPB and control scenario, where there has been a shift in the species composition trajectory following MPB mortality.

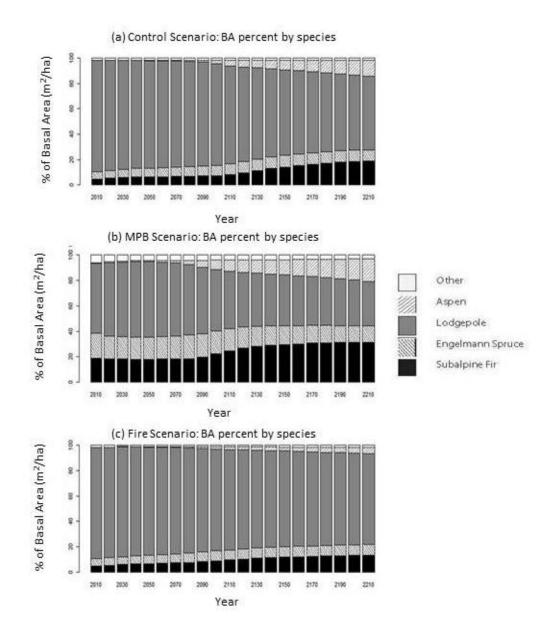


Figure 5.5 (a-c) Average Species Composition by Percent of Basal Area. Percent of basal area (in m²/Ha) species trajectories for each simulation averaged across all plots where a.) is the percent basal area for each species in the MPB scenario, b.)is the Control scenario and c.) is the Fire scenario

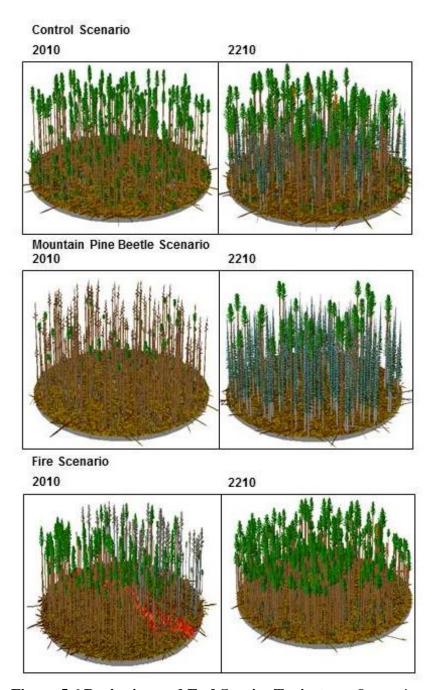


Figure 5.6 Beginning and End Species Trajectory. Output images from FVS showing the differences in stand composition trajectories over time for each scenario for field plots initially dominated by a lodgepole overstory and an understory of subalpine fir the MPB and Control model scenarios.

5.5 Impacts of Simulated Fire Disturbance on Stand Structure

In 2010, the fire scenario was primarily lodgepole pine in the overstory, with an average 87.9% of the remaining basal area represented by lodgepole after the simulated fire. The simulated fire stand structure looked somewhat different from the MPB or control scenario simulations in 2210 overall averaged across plots. As shown in figure 5.5c., the live overstory was dominated by 71.6% lodgepole pine, 13% of the basal area consisted of subalpine fir, 5.1% was aspen and 8.4% was Engelmann spruce, leaving 1.5% of basal area as other species. The fire scenario had the most percentage of basal area represented by lodgepole out of the three scenarios in 2210.

In 2010, a real fire burned through two plots. Every tree was killed, and no regeneration was present during the 2011 resurvey. There was some herbaceous cover present along the fuels transects. Much of the standing live carbon was transferred to the standing or downed dead carbon pools, which changes the stand structure. This transfer of carbon to the ground level pools may have impacts on soil and regeneration processes in the near and long term. The fire I simulated to consume 72% of basal area was a conservative estimate, as the real fire consumed almost all of the basal area in the two plots.

5.6 Variation in Plots for Carbon and Stand Structure Trajectories

The 119 field plots were split up between primary overstory and understory species composition, as described in the methods section, to investigate variation

in carbon and species composition between plot types as opposed to averages of carbon and stand composition trajectories across all plots. The plots were split up based on the species composition observed in plots in 2010, and thus included MPB mortality. Figures 5.7-5.10 show an example of the differences in the four carbon pool trajectories for the three plot types for the MPB scenario. These stand types were investigated for the MPB scenario to compare the individual plot species compositions and carbon trajectories between scenarios by primary overstory and understory species composition. Only the MPB scenario was split up into plot types because the MPB scenario represented reality, where stand composition types were qualified in the field after MPB disturbance, and thus would not reflect valid species composition necessarily for the other two simulated scenarios.

5.6.1 Variation in Carbon Trajectories between Plot Types

There were differences in carbon storage in some of the plots within the MPB scenario due to changes in stand structure, which is shown in figure 5.7-5.11. Of the three main types of plots, the third type of plot, which consisted of an overstory and understory dominated by subalpine fir, stored more carbon than the average across all plots in the standing live carbon pool (where the calculated confidence interval for type 3 plots did not intersect the other values for 2010, validating a statistically significant difference). The average for these 7 plots in 2210 was 136.9 Mg/ha standing live carbon. The first type of plot, with a

lodgepole-dominated overstory and a subalpine fir-dominated understory, the standing live pool stored less than the average stored across all plots at 130.5 Mg/ha. The second type of plot, where lodgepole dominated both the overstory canopy and the understory, there was a majority of 79 plots in this category, was about the same as the average across all plots.

MPB Scenario: Standing Live Carbon

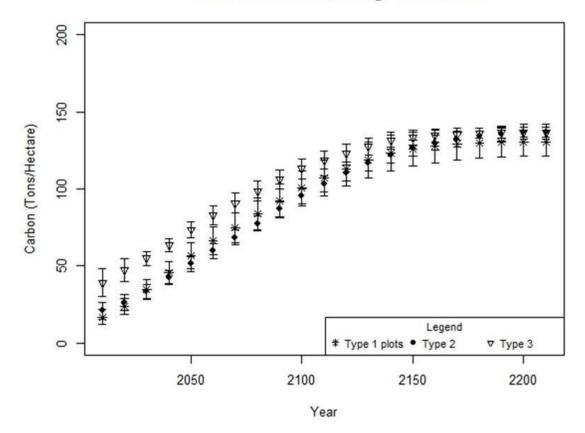


Figure 5.7 Standing Live Carbon by Plot Type. Shows variability in carbon stored within the standing live carbon pool between the different plot types in the MPB scenario.

MPB Scenario: Standing Dead Carbon

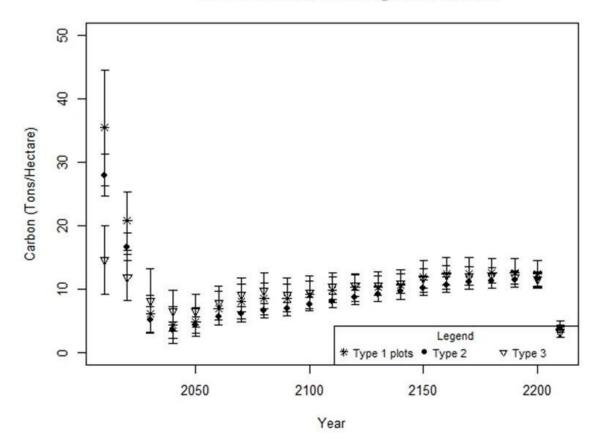


Figure 5.8 Standing Dead Carbon by Plot Type Variability within the standing dead carbon pool between the different plot types in the MPB scenario.

MPB Scenario: Downed Dead Carbon

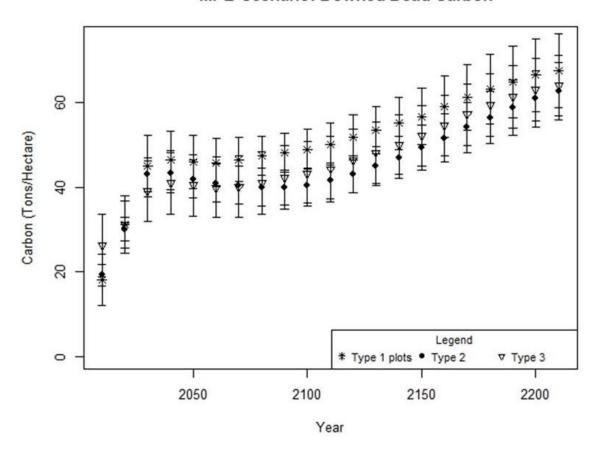


Figure 5.9 Downed Dead Carbon by Plot Type. Variability in carbon stored within the downed dead carbon pool between the different plot types in the MPB scenario.

MPB Scenario: Total Stand Carbon

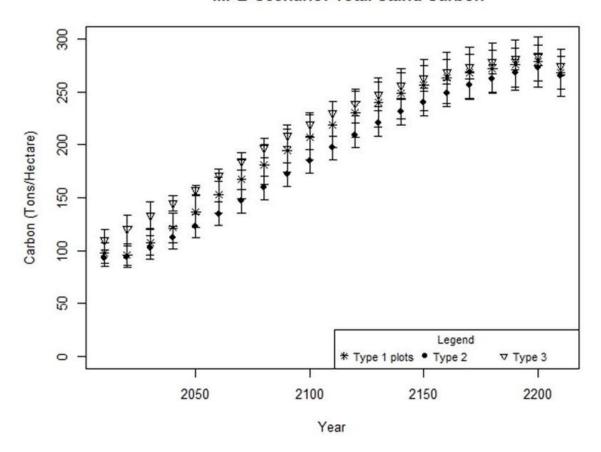


Figure 5.10 Total Stand Carbon by Plot Type. Variability in total stand carbon storage between the different plot types in the MPB scenario.

5.6.2 Variation in Stand Composition Trajectories between Plot Types

For the MPB scenario (as shown in figure 5.11 a-c), when the plots are split into the three species type categories, the stand trajectories for species varied somewhat. Type 1 plots initially were dominated in the overstory vegetation by lodgepole (45%) and subalpine fir (31.4%), and in 2210, are dominated by 62.3% of the basal area by subalpine fir. Engelmann spruce occupy 19.5% of the basal area in type 1 plots in 2210, and 11.8% is lodgepole on average. Type 2 plots were initially dominated by lodgepole in 2010 accounting for 65% of basal area, which was reduced to 43.8% by 2210. This was offset by an increase in subalpine fir, which began at 6.3% in 2010 and increased to representing 19.2% in 2210, as well as aspen, which increased from less than 1% in 2010 to almost 23% in 2210. Type 3 plots were initially dominated by subalpine fir, which only increased from 70% to 79% of basal area between 2010 and 2210. These plots experienced a decrease in lodgepole from 11.9% to 8.5% basal area from 2010 to 2210. Engelmann spruce was reduced over time from 2010 to 2210 by representing 18.2% to 11.8% of basal area.

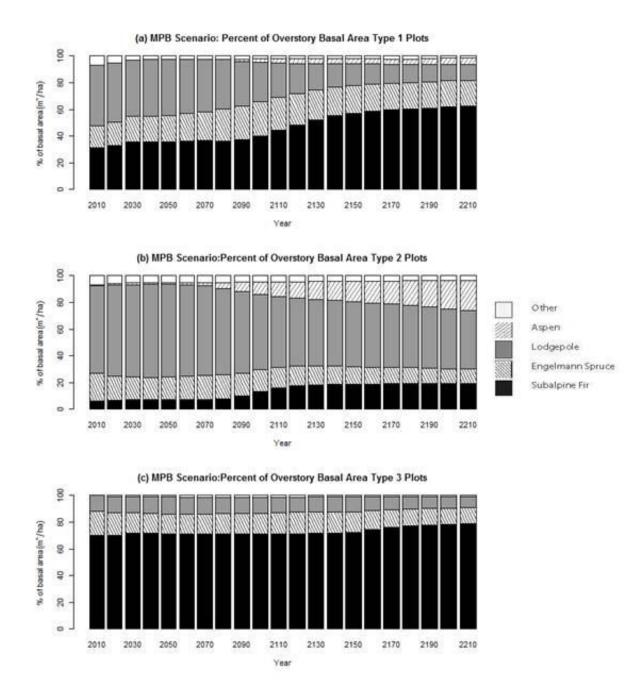


Figure 5.11 (a.-c) Species Trajectories between Plot Types. Species trajectory projections by type 1, 2 or 3 species plots over time for the MPB scenario.

VI. DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS

This research stands to track and compare carbon and species succession trajectories without disturbance, after a real MPB disturbance, and after a simulated fire, in order to better quantify the impacts of large disturbances on carbon and species, in order to provide better information to forest managers. I used forest inventory data collected in field plots to initialize the FVS model to quantify initial and future carbon and species composition trajectory projections. This data provided information on how differing disturbances, which may increase with global climate change, may change carbon and species trajectories and provides insight into how to manage forests better. The MPB outbreak in the Southern Rocky Mountains has altered the trajectory of carbon storage and species composition in Southern Rocky Mountain forests. The surveyed field plots were dominated by lodgepole, where most of the larger-diameter lodgepole were killed by MPB (unlike fire disturbances, where size is not typically selected). As disturbances are predicted to increase in frequency and severity in a warming climate, the intricate relationship between carbon storage and species composition, and how trajectories change due to disturbance, will become ever-important. These results showed carbon storage and species composition are altered after insect disturbances, and are different from the impacts on stand structure and carbon storage from fire disturbances. Further, carbon storage may differ between species types present in stands.

6.1 Impacts of MPB on Carbon Storage

Stand carbon storage trajectories were altered short-term as a result of the MPB disturbance. The immediate impacts of MPB outbreaks on carbon storage are substantial, causing a rapid transfer of 27.1 Mg/Ha, or 28.6% of the total stand carbon from the standing live pool to the standing dead pool and subsequently to the downed dead pool. However, these pools recover at varying rates following MPB outbreaks. Klutsch et al. (2009) found a 69% reduction in overall basal area, and transfers from the standing live carbon pool to the standing dead and downed dead/litter pools for northern Colorado lodgepole forests experiencing MPB epidemic conditions. This differed from the field plots collected for my research, where an average 72% of basal area was lost. I found that the impacts on the standing live pool were relatively short-lived and that standing live carbon recovered to pre-outbreak conditions by 2060 (roughly 60 Mg/ha). The total stand stored carbon returns to pre-outbreak conditions by 2040. After about 90 years, differences in carbon storage in all the carbon pools were negligible between the two scenarios.

In contrast to this study, Pfeifer et al. (2010) examined stand carbon changes in a northern Idaho forest as a result to a beetle outbreak. They observed a rebound in carbon to pre-outbreak conditions in 25 years. Mortality of basal area was not as high for their region and the forest had slightly different stand characteristics, such as the presence of whitebark pine (*Pinus albicaulis*) and more

Douglas fir (*Pseudotsuga menziesii var. menziesii*). Pfeifer et al. validates the notion that forest recovery of carbon storage to pre-outbreak conditions is not only possible, but occurs over a relatively short time span.

The trajectories of the field plots by the dominant species present in the overstory and understory varied somewhat in carbon content and species composition. This study only split plots based on their dominant overstory and understory vegetation, and not any other factors, such as stand densities or diameter distributions of trees. As modeled for "actual conditions" in the MPB scenario, the 7 plots dominated by subalpine fir in both the overstory and understory, or the type 3 plots, stored above the average amount of carbon stored in all plots. This may indicate that subalpine fir has a greater carbon storage potential in this ecosystem. Initially, type 1 plots had higher standing dead carbon storage, indicating potentially higher percent basal area impacted by MPB. Type 3 plots had the lowest storage in the standing dead carbon pool, which is intuitive in that they primarily consist of non-host species for MPB. Type 3 plots stored more carbon on average in the downed dead pool than the other plots.

6.2 Impacts of Simulated Fire Disturbance on Carbon Storage

Both MPB and fire disturbances altered the trajectories of carbon storage, however a fire that burns the same area MPB affects seems to impact carbon pools more severely and for a longer time period. For all 200 years of the simulation, the fire scenario stored less carbon in the standing live, standing dead and total stand

carbon pools compared to the other scenarios. This could have been due to the fire consuming surface fuels in the downed-dead wood biomass pools and smaller seedlings and saplings that remained in place during the MPB simulation. The fire scenario showed higher carbon storage in the standing dead pool than the other scenarios. This shows how the fire impacts stands differently, where doesn't impacts selective species or size classes. Downed dead carbon was significantly lower in the fire scenario by 2210. Initially, downed dead carbon was projected in 2020 to be similar to that stored in the downed dead pool in the MPB scenario. By 2030, however, downed dead carbon stored was lower in the fire scenario than in the MPB scenario. It seems that more carbon, likely from the standing dead pool, is transferred to the downed dead pool over a longer time period in MPB disturbances and more of the carbon from the standing dead pool is transferred over time to the other pools in fire disturbances over time.

The total carbon storage recovered to pre-fire levels more slowly than the MPB scenario recovered to pre-MPB storage, where carbon returned to pre-fire carbon storage in the standing live pool and total stand carbon by 2080 which was twenty years later than recovery of the MPB disturbance trajectory.

6.3 Impacts of MPB on Stand Structure

MPB disturbances impact stand structure differently than other major disturbances, such as fire or wind, because only select trees, specifically older lodgepole with a greater DBH, are taken out of the live biomass pool. Insect

disturbances allow seed dispersal, light and water to interact differently within the forest compared to an even-aged, undisturbed forest. This allows for differences in stand structure and species composition between disturbed and undisturbed forests of the same type. Changes in stand composition also can subsequently change the rate at which carbon is sequestered and stored, as different species sequester carbon at different rates and ages of development. Initially, an average 72% of basal area was killed by mountain pine beetle in this study area. This corresponds to Klutsch et al. (2009) where the live basal area declined 71% in their beetle infested study plots in the Colorado Arapaho National forest.

Succession was modeled conservatively by projecting the current trajectories with only advanced regeneration, out 200 years, but there was still a shift in species composition over time in the MPB scenario as compared to the control scenario. If the MPB outbreak had not occurred, species composition would be dominated by primarily lodgepole pine. The MPB scenario however, shows a species composition shift towards a greater percentage of the basal area being subalpine fir. A mixed vegetation composition in the future could be beneficial for ecological sustainability as it encourages biodiversity, which will make stands more resilient.

This observation is supported through the study carried out by Collins et al. (2011) that showed a shift towards a subalpine-fir dominated canopy in Colorado in untreated stands affected by MPB through the use of vegetation modeling.

Collins et al (2011) found that tree regeneration in MPB impacted lodgepole stands were more evenly distributed with subalpine fir and lodgepole pine as well. This validates a landscape level increase in basal area represented by subalpine fir after a MPB outbreak, for a more mixed stand composition. Klutsch et al. (2009) also concluded that stands impacted by the mountain pine beetle epidemic will result in an uneven aged stand structure consisting of older, existing lodgepole and younger subalpine fir and Engelmann spruce. Their work along with this study suggest that future stand composition depends heavily on advance regeneration present at the time of disturbance.

6.4 Impacts of Simulated Fire Disturbance on Stand Structure

Based on the FVS model results, fire seems to encourage a stand structure trajectory that becomes dominated by primarily lodgepole pine, which is different from the trajectories of species composition in the absence of disturbance and after MPB disturbance. These findings correspond with known successional trends where pure lodgepole stands typically regenerate after stand-replacing fires in forests that were dominated by lodgepole (Lotan et al. 1985). Even in places where forests are dominated by spruce and fir, lodgepole can increase following fires. In the absence of fire though, subalpine fir and Englemann spruce increase in dominance where there have been fewer fires (Romme and Knight 1981).

In the fire scenario, the dominant species in plots makes a difference in the stand composition trajectories over time.

6.5 Conclusions and Recommendations

6.5.1 Conclusions

Changes to carbon storage in forests affected by MPB were relatively short-lived under scenarios that did not incorporate further disturbances. Standing live carbon rebounded within 50 years in most stands. However, species composition changed over a longer time period, and there were substantial differences in forest stand structure and species composition that persisted after 200 years of simulation. MPB disturbances impact stand structure differently than other major disturbances, such as fire. MPB targets older, large diameter lodgepole pines, leaving behind advanced regeneration that grow rapidly in the years after disturbance. This resulted in standing-live carbon stocks recovering quickly after MPB. This was accompanied by changes in species composition trajectories, with a slight shift toward more aspen, fir, and spruce. Succession modeling was conservatively, however there was still a shift in species composition over time in the MPB simulation, compared to the control simulation. The findings of this study corroborate those found by Collins et al. (2011), who showed a shift towards a subalpine-fir dominated canopy in Colorado in untreated stands affected by MPB through the use of vegetation modeling. Lodgepole pine forests affected by MPB appear to enter a self-correcting mode, where a more diverse forest develops after MPB disturbance, making it less susceptible to future MPB disturbances. Carbon storage differs within each scenario as well, based on

dominant overstory and understory vegetation, where plots dominated in the over and understory by subalpine fir trajectories store more carbon than other plots.

In lodgepole pine forests, fire affects the larger trees favored by beetles, but also causes mortality in advanced regeneration. Carbon loss during a fire is a function of fuel loads and fire severity and recovery of carbon after a fire is a function of seed availability and regeneration rates. The results from this study and those found in the literature, suggest that burned lodgepole pine forests will regenerate as lodgepole, and the rate of carbon recovery is somewhat slower after fire than after the MPB outbreak. Fires perpetuating lodgepole pine in stands could make the ecosystem more vulnerable to disturbances in the future.

These changes in both carbon and species composition may have additional effects on carbon cycling by altering primary productivity, soil biogeochemistry, and regeneration over time; processes that warrant further investigation.

6.5.2 Recommendations and Management Implications

This research suggests that disturbances change forest composition and carbon trajectories over time, and that different disturbances alter these trajectories differently. Also, this research concluded that there are differences in the trajectories between individual stands within forest types that are impacted by disturbance. The local scale impacts of MPB outbreaks are substantial and could have implications for how forests offset greenhouse gas emissions and global climate change at broader scales. It would be beneficial for stakeholders managing

for carbon storage and sequestration in forests to account for the varying carbon impacts and the length of recovery time in carbon pools resulting from the various disturbances that affect forests. This is especially important as disturbances are projected to increase in a warming climate. Managers should also account for the differences that may occur in between stands across a landscape scale, and that a uniform management design may not be optimal across an entire landscape, as there are variances between stands and species composition types.

REFERENCES

- Amman, G. D. 1977. The role of mountain pine beetle in lodgepole ecosystems:

 Impact on succession Pages 3-18 *in* W. J. Mattson, editor. The Role of

 Arthropods in Forest Ecosystem. Springer-Verlag, New York.
- Aoki, C. F., W. H. Romme, and M. E. Rocca. 2011. Lodgepole Pine Seed

 Germination Following Tree Death from Mountain Pine Beetle Attack in

 Colorado, USA. The American Midland Naturalist **165**:446-451.
- Avery, T. E. and H. E. Burkhart. 2002. Forest Measurements. 5 edition. McGraw Hill, NY, NY.
- Baker, W. L. and T. T. Veblen. 1990. Spruce Beetles and Fires in the Nineteenth-Century Subalpine Forests of Western Colorado, U.S.A. Arctic and Alpine Research 22:65-80.
- Barrow, E. and G. Yu. 2005. Climate Scenarios for Alberta. Prairie Adaptation Research Collaborative (PARC).
- Bazzaz, F. A. 1996. Plants in Changing Environments. Cambridge University Press, U.K.
- Bentz, B. J., J. Régnière, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold. 2010. Climate Change and Bark

- Beetles of the Western United States and Canada: Direct and Indirect Effects. BioScience **60**:602-613.
- Bessie, W. C. and E. A. Johnson. 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. Ecology **76**:747-762.
- Birdsey, R., K. Pregitzer, and A. Lucier. 2006. Forest Carbon Management in the United States. Journal of Environment Quality **35**:1461.
- Birdsey, R. A. 1992. Carbon storage and accumulation in United States forest ecosystems. Gen. Tech. Rep. WO-59, Washington D.C.: U.S. Department of Agriculture, Forest Service, Washington Office.
- Bradford, J. B., R. A. Birdsey, L. A. Joyce, and M. G. Ryan. 2008. Tree age, disturbance history, and carbon stocks and fluxes in subalpine Rocky Mountain forests. Global Change Biology **14**:2882-2897.
- Breshears, D. and C. D. Allen. 2002. The importance of rapid, disturbance-induced losses in carbon management and sequestration. Global Ecology & Biogeography 11:1-5.
- Brown, J., editor. 1975. Fire cycles and community dynamics in lodgepole pine forests.
- Carroll, A. L., S. W. Taylor, J. Regniere, and L. Safranyik. 2003. Effect of climate change on range expansion by the mountain pine beetle in British Columbia. Page Paper 195.

- CCSP. 2007. The First State of the Carbon Cycle Report (SOCCR): The North

 American Carbon Budget and Implications for the Global Carbon Cycle.

 National Oceanic and Atmospheric Administration, National Climatic Data

 Center, Asheville, NC.
- Chapin III, F. S., P. A. Matson, and H. Mooney. 2002. Principles of terrestrial ecosystem ecology. Springer-Verlag, New York.
- Claveau, Y., C. Messier, P. G. Comeau, and K. D. Coates. 2002. Growth and crown morphological responses of boreal conifer seedlings and saplings with contrasting shade tolerance to a gradient of light and height. Canadian Journal of Forest Research 32:458-468.
- Collins, B. J., C. C. Rhoades, R. M. Hubbard, and M. A. Battaglia. 2011. Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands. Forest Ecology and Management **261**:2168-2175.
- Comeau, P. and J. P. Kimmins. 1989. Above- and below-ground biomass and production of lodgepole pine on sites with differing soil moisture regimes.

 Canadian Journal of Forest Research 19:447-454.
- Crookston, N. and G. Dixon. 2005. The forest vegetation simulator: A review of its structure, content, and applications. Computers and Electronics in Agriculture **49**:60-80.

- Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D.
 Flannigan, P. J. Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D.
 Simberloff, F. J. Swanson, B. J. Stocks, and B. Michael Wotton. 2001.
 Climate Change and Forest Disturbances. BioScience 51:723-734.
- Diskin, M., M. E. Rocca, K. N. Nelson, C. F. Aoki, and W. H. Romme. 2011.

 Forest developmental trajectories in mountain pine beetle disturbed forests of Rocky Mountain National Park, Colorado. Canadian Journal of Forest Research 41:782-792.
- Dixon, G. E. 2003. Essential FVS: a user's guide to the Forest Vegetation

 Simulator., USDA-Forest Service, Forest Management Service Center, Fort

 Collins, CO.
- Fahey, T. J. and D. H. Knight. 1986. Lodgepole Pine Ecosystems. BioScience **36**:610-617.
- Flannigan, M. D., B. J. Stocks, and B. M. Wotton. 2000. Climate change and forest fires. The Science of the Total Environment **262**:221-229.
- Franklin, J. F., T. A. Spies, R. V. Pelt, A. B. Carey, D. A. Thornburgh, D. R. Berg, D. B. Lindenmayer, M. E. Harmon, W. S. Keeton, D. C. Shaw, K. Bible, and J. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management **155**:399-423.

- Friedlingstein, P., L. Bopp, P. Ciais, J. Dufresne, Louis, L. Fairhead, H. LeTreut, P. Monfray, and J. Orr. 2001. Positive feedback between future climate change and the carbon cycle. Geophys. Res. Lett. **28**:1543-1546.
- Glenn-Lewin, D. C., R. K. Peet, and T. T. Veblen, editors. 1992. Plant Succession: Theory and Prediction. Chapman and Hall, London, UK.
- Goward, S. N., J. G. Masek, W. Cohen, G. Moisen, G. J. Collatz, S. Healey, R. A.
 Houghton, C. Huang, R. Kennedy, B. Law, S. Powell, D. Turner, and M.
 A. Wulder. 2008. Forest Disturbance and North American Carbon Flux.
 EOS Transactions American Geophysical Union 89:105.
- Hamann, A. and T. Wang. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia Ecology **87**:2773-2786.
- Heal, G. 2000. Valuing Ecosystem Services. Ecosystems 3:24-30.
- Heath, L. S. and J. E. Smith. 2004. 2003 Report on Sustainable Forests:

 Contribution of forest ecosystems fo the total global carbon budget, including absorption and release of carbon USDA Forest Service.
- Hurteau, M. and M. North. 2008. Fuel treatment effects on tree-based forest carbon storage and emissions under modeled wildfire scenarios. Frontiers in Ecology and the Environment 7:409-414.
- Hurteau, M. and M. North. 2009. Fuel treatment effects on tree-based forest carbon storage and emissions under modeled wildfire scenarios. Frontiers in Ecology and the Environment **7**:409-414.

- Hurtt, G. C., S. W. Pacala, P. R. Moorcroft, J. Caspersen, E. Shevliakova, R. A.Houghton, and B. Moore. 2002. Projecting the future of the U.S. carbon sink. Proceedings of the National Academy of Sciences 99:1389-1394.
- IPCC. 2007. Intergovernmental Panel on Climate Change Assessment Report.

 Cambridge University Press, Cambridge, United Kingdom and New York,

 NY, USA.
- Joyce, L. A. and R. Birdsey. 2000. The impact of climate change on America's forests: a technical document supporting the 2000 USDA Forest Service RPA Assessment. . U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO:.
- Kashian, D. M., D. B. Tinker, M. G. Turner, and F. L. Scarpace. 2004. Spatial heterogeneity of lodgepole pine sapling densities following the 1988 fires in Yellowstone National Park, Wyoming, U.S.A. . Canadian Journal of Forest Research:2263-2276.
- Kashian, D. M., W.H. Romme, D.B. Tinker, M.G. Turner, and M.G. Ryan. 2006.

 Carbon storage on landscapes with stand-replacing fires. BioScience **56**: 598-606.
- Kimball, B. A., J. R. Mauney, F. S. Nakayama, and S. B. Idso. 1993. Effects of increasing atmospheric CO₂ on vegetation. Plant Ecology **104-105**:65-75.
- Klutsch, J. G., J. F. Negrón, S. L. Costello, C. C. Rhoades, D. R. West, J. Popp, and R. Caissie. 2009. Stand characteristics and downed woody debris

- accumulations associated with a mountain pine beetle (Dendroctonus ponderosae Hopkins) outbreak in Colorado. Forest Ecology and Management **258**:641-649.
- Kueppers, L. and J. Harte. 2005. Subalpine Forest Carbon Cycling: Short- and Long-Term Influence of Climate and Species. Ecological Applications **15**:1984-1999.
- Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L.
 Carroll, T. Ebata, and L. Safranyik. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452:987-990.
- Lal, R. 2004. Soil Carbon Sequestration Impacts on Global Climate Change and Food Security. Science:1623-1627.
- Lal, R., J. M. Kimble, R. F. Follett, and B. A. Stewart, editors. 2000. Assessment Methods for Soil Carbon. CRC/Lewis Publishers, Boca Raton, FL.
- Lamlom, S. H. and R. A. Savidge. 2003. A reassessment of carbon content in wood: variation within and between 41 North American species. Biomass and Bioenergy **25**:381-388.
- Lotan, J. 1976. Cone Serotiny Fire Relationships in Lodgepole Pine.*in* Tall

 Timbers Fire Ecology Conference Proceedings, Tall Timbers Research

 Center, Tallahassee, FL.
- Lotan, J., J. Brown, and L. Neuenschwander., editors. 1985. Role of fire in lodgepole pine forests, Washington State University, Pullman.

- Lotan, J. E. and W. B. Critchfield. 2004. Lodgepole Pine. USFS.
- Lotan, J. E. and D. A. Perry. 1983. Ecology and regeneration of lodgepole pine., Washington D.C. .
- Lutes, D. C., R. E. Keane, J. F. Caratti, C. H. Key, N. C. Benson, S. Sutherland, and L. J. Gangi. 2006. FIREMON: Fire Effects Monitoring and Inventory System. Technical RMRS-GTR-164-CD.
- Marschner, P. and Z. Rengel, editors. 2007. Nutrient Cycling in Terrestrial Ecosystems. Springer-Verlag, Berlin, Heidelberg.
- Mladenoff, D. 2004. LANDIS and forest landscape models. Ecological Modelling **180**:7-19.
- Monserud, R. A. Y., Yuqing; Huang, Shongming; Tchebakova, Nadja. 2008.

 Potential change in lodgepole pine site index and distribution under climatic change in Alberta Canadian Journal of Forest Research 38:343-352.
- Monson, R. K., A. A. Turnipseed, J. P. Sparks, P. C. Harley, L. E. Scott-Denton, K. Sparks, and T. E. Huxman. 2002. Carbon sequestration in a high-elevation, subalpine forest. Global Change Biology 8:459-478.
- Newell, R. G. and R. N. Stavins. 2000. Climate Change and Forest Sinks: Factors

 Affecting the Costs of Carbon Sequestration. Journal of Environmental

 Economics and Management 40:211-235.

- Pacala, S. W., R. A. Birdsey, S. D. Bridgham, R. T. Conant, K. Davis, B. Hales, R. A. Houghton, J. C. Jenkins, M. Johnston, G.Marland, and K. Paustian.
 2007. The North American Carbon Budget Past and Present. In: The First State of the Carbon Cycle Report (SOCCR): The North American Carbon Budget and Implications for the Global Carbon Cycle. U.S. Climate
 Change Science Program and the Subcommittee on Global Change
 Research. National Oceanic and Atmospheric Administration, National
 Climatic Data Center, Asheville, NC, USA.
- Parker, A. J. and K. C. Parker. 1983. Comparative successional roles of trembling aspen and lodgepole pine in the Southern Rocky Mountains.
- Parton, W. J. 1996. The CENTURY model. Pages 283–293 *in* D. S. Powlson, P. Smith, and J. U. Smith, editors. Evaluation of Soil Organic Matter Models Using Existing Long-Term Datasets. Springer-Verlag, Heidelberg
- Pfeifer, E. M., J. A. Hicke, and A. J. H. Meddens. 2011. Observations and modeling of aboveground tree carbon stocks and fluxes following a bark beetle outbreak in the western United States. Global Change Biology 17:339-350.
- Prentice, I. C., G.D. Farquhar, M.J.R. Fasham, M.L. Goulden, M. Heimann, V.J. Jaramillo, H.S. Kheshgi, C. Le Quéré, D. W. R. W. R.J. Scholes, D. Archer, M.R. Ashmore, O. Aumont, D. Baker, M. Battle, M. Bender, L.P. Bopp, P. Bousquet, K. Caldeira, P. M. C. P. Ciais, W. Cramer, F.

Dentener, I.G. Enting, C.B. Field, P. Friedlingstein, E.A. Holland,, J. I. H. R.A. Houghton, A. Ishida, A.K. Jain, I.A. Janssens, F. Joos, T. Kaminski, C.D. Keeling, D. W. K. R.F. Keeling, K.E. Kohfeld, W. Knorr, R. Law, T. Lenton, K. Lindsay, E. Maier-Reimer,, R. J. M. A.C. Manning, A.D. McGuire, J.M. Melillo, R. Meyer, M. Mund, J.C. Orr, S. Piper, K. Plattner,, and S. S. P.J. Rayner, R. Slater, S. Taguchi, P.P. Tans, H.Q. Tian, M.F. Weirig, T. Whorf, A. Yool. 2001. The Carbon Cycle and Atmospheric Carbon Dioxide. Pages 183-285 *in* J. T. Houghton, editor. Cambridge University Press, Cambridge.

- Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale Drivers of Natural DisturbancesProne to Anthropogenic Amplification: The Dynamics of Bark BeetleEruptions. BioScience 58:501-517.
- Rapp, V. 2004. Western Forests, Fire Risk, and Climate Change. Page 12. Forest Service, U.S.Department of Agriculture, Portland, OR: Pacific Northwest Research Station.
- Roe, A. L. and G. D. Amman. 1970. Mountain Pine Beetle in Lodgepole Pine Forests. Research Paper INT-71, USDA Forest Service, Intermountain Research Station.
- Rollins, M. G. 2009. LANDFIRE-a nationally consistent vegetation, wildland fire, and fuel assessment. International Journal of Wildland Fire 18.

- Romme, W. H. 1982. Fire and Landscape Diversity in Subalpine Forests of Yellowstone National Park. Ecological Monographs **52**:199-221.
- Romme, W. H. and D. H. Knight. 1981. Fire Frequency and Subalpine Forest Succession Along a Topographic Gradient in Wyoming. Ecology **62**:319-326.
- Romme, W. H., D. H. Knight, and J. B. Yavitt. 1986. Mountain Pine Beetle

 Outbreaks in the Rocky Mountains: Regulators of Primary Productivity?

 The American Naturalist 127:484-494.
- Running, S. W. 2008. Ecosystem Disturbance, Carbon, and Climate. Science **321**:652-653.
- Ryan, M., M. Harmon, R. Birdsey, C. Giardina, L. Heath, R. Houghton, R. Jackson, D. McKinley, J. Morrison, BC Murray, D. Pataki, and K. Skog. 2010. A Synthesis of the Science on Forests and Carbon for U.S. Forests. Ecological Society of America, Issues In Ecology 13:1-16.
- Safranyik, L., A. L. Carroll, J. Régnière, D. W. Langor, W. G. Riel, T. L. Shore, B.
 Peter, B. J. Cooke, V. G. Nealis, and S. W. Taylor. 2010. Potential for
 Range Expansion of Mountain Pine Beetle into the Boreal Forest of North
 America. The Canadian Entomologist 142:415-442.
- Schmoldt, D. L., David L. Peterson, R. E. Keane, J. M. Lenihan, D. McKenzie, D. R. Weise, and D. V. Sandberg. 1999. Assessing the Effects of Fire

Disturbance on Ecosystems: A Scientific Agenda for Research and Management. USFS, Pacific Northwest

Research Station.

- Sibold, J. S., T. T. Veblen, K. Chipko, L. Lawson, E. Mathis, and J. Scott. 2007.
 Influences of Secondary Disturbances on Lodgepole Pine Stand
 Development In Rocky Mountain National Park Ecological Applications
 17:1638-1655.
- Siegenthaler, U. and J. L. Sarmiento. 1993. Atmospheric carbon dioxide and the ocean. Nature **365**:119-125.
- Sitch, S., C. Huntingford, N. Gedney, P. E. Levy, M. Lomas, S. L. Piao, R. Betts,
 P. Ciais, P. Cox, P. Friedlingstein, C. D. Jones, I. C. Prentice, and F. I.
 Woodward. 2008. Evaluation of the terrestrial carbon cycle, future plant
 geography and climate-carbon cycle feedbacks using five Dynamic Global
 Vegetation Models (DGVMs). Global Change Biology 14:2015-2039.
- Smith, T. M., W. P. Cramer, R. K. Dixon, R. Leemans, R. P. Neilson, and A. M. Solomon. 1993. The Global Terrestrial Carbon Cycle. Water, Air and Soil Pollution 70:19-37.
- Son, E., a J.-J. Kim,b Y.W. Lim,c T.T. Au-Yeung,a C.Y.H. Yang,a C. Breuila 2010. Diversity and decay ability of basidiomycetes isolated from lodgepole pines killed by the mountain pine beetle. Canadian Journal of Microbiology **57**:33-41.

- Stage, A. R. 1973. Prognosis model for stand developement. USDA Forest Service, Ogden, UT Intermountain Forest and Range Experiment Station.
- Stohlgren, T. J. and R. R. Bachand. 1997. Lodgepole Pine (*Pinus contorta*)

 Ecotones in Rocky Mountain National Park, Colorado, USA Ecology

 78:632-641.
- Swift, R. S. 2001. Sequestration of Carbon By Soil. Soil Science 166:858-871.
- Tallis, H., T. Ricketts, E. N. Driss Ennaanay, Kari Vigerstol, Guillermo Mendoza,
 N. O. Stacie Wolny, Juliann Aukema, John Foster, Jessica Forrest, Dick
 Cameron,, and K. Arkema. 2008. InVEST 1.003 beta User's Guide.
 Stanford.
- Thorsell, J. and T. Sigaty. 1997. A Global Overview of Forest Protected Areas on the World Hertitage List Natural Heritage Programme, IUCN, Gland, Switzerland.
- USFS. 2009. Forest Health Damage Detection Surveys Acres with Mortality.

 USDA Forest Service.
- Veblen, T. T., K. S. Hadley, M. S. Reid, and A. J. Rebertus. 1989. Blowdown and stand development in a Colorado subalpine forest. Canadian Journal of Forest Research 19:1218-1225.
- Vose, J. 2006. Forest Carbon Cycling. Encyclopedia of Environmetrics. John Wiley & Sons, Ltd.

- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006.

 Warming and Earlier Spring Increase Western U.S. Forest Wildfire

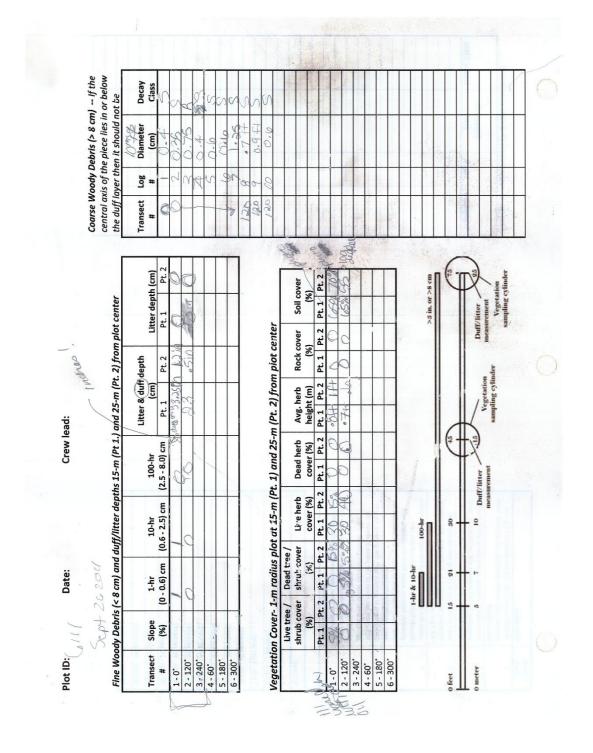
 Activity. Science **313**:940-943.
- Westerling, A. L., M. G. Turner, E. A. H. Smithwick, W. H. Romme, and M. G. Ryan. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. Proceedings of the National Academy of Sciences 108:13165-13170.
- Whelan, R. J. 1995. The Ecology of Fire. Cambridge University Press, UK.
- White, M. A., P. E. Thornton, S. W. Running, and R. R. Nemani. 2000.
 Parameterization and Sensitivity Analysis of the BIOME–BGC Terrestrial
 Ecosystem Model: Net Primary Production Controls. Earth Interactions
 4:1-85.
- Wigley, T. M. L. and D. S. Schimel, editors. 2000. Constraints on the atmospheric carbon budget from spatial distributions of CO2. Cambridge University Press, Cambridge, UK.
- Winjum, J. K., R. K. Dixon, and P. E. Schroeder. 1992. Estimating the global potential of forest and agroforest management practices to sequester carbon. Water, Air, & Dixon, and P. E. Schroeder. 1992. Estimating the global potential of forest and agroforest management practices to sequester carbon. Water, Air, & Dixon, and P. E. Schroeder. 1992. Estimating the global potential of forest and agroforest management practices to sequester carbon.
- Zhu, Z., C. Key, D. Ohlen, and N. Benson. 2006. Evaluate Sensitivities of Burn-Severity Mapping Algorithms for Different Ecosystems and Fire Histories

in the United States. USGS, National Center for Earth Resources Observation and Science, Sioux Falls, SD.

Appendix I. Raw field data from 2 plots impacted by fire

														Day	,	Com	00														
	- Down	3	Red	Deed	7	Del	7	20	Down	Dead	Dead	Bollen	7	Gom/	Deed																
	1	Del	9	d	2	ð	d	d	Ã	D	0	3	Dest	Š	9	ď	å			_	_	_	_	_	_	_	_		_	_	_
Bearing to plot center	39	49	62	112	135	154	162	163	229	235	263	262	289	320	333	345	348														
plot center Bearing to (m) plot center	3.03	3.17	8	4.61	5.3	3.76	5.36	70.7	4.65	4.5	7.07	7.28	3.68	5.38	5:55	4.09	3.34														
# years dead	6+ years ago: both small and large twigs not rema				4 years ago: no needles remaining but small and			4 years ago: no needles remaining but small and	4 years ago: no needles remaining but small and			4 years ago: no needles remaining but small and		6+ years ago: both small and large-twigs not rema		5 years ago: only large twigs remaining	5 years ago: only large twigs remaining											×			
Mort	n				D			-	n			n	Maria	n		n	n														
ecayCl																															
wthRt	4	×	×	×	m	×	×	2	2	×	×	2	×	5	×	3	3														
ge Gr	H					_		-	_	_		_	H									_									_
rBHt Ag	0	0	2.5	2	0	1.8	2	1.8	8.6	9.0	0.8	11.2	-	0	0	0	3.6														
rPct LIC	0	0	09	09	0	20	40	0	0	09	20	0	80	0	20	0	0									-			Н		
LIC	1	6		10		-	-	2	4	6		18	4		2	7	2														
Heigh	5.1	11.9	*			17.1	15.1	16.2	11.4	12.9			17.4		20.2	11.7	11.5	7	5.5			16									
DBH	17	22	16	14	11	22	21	48	16	17	19	17	33	14	33	19	19	1						,,							
TagNo Species TreeStat DBH Heignt LiCrPct LiCrBHt Age GrwthRt DecayCl Mort	Q	I	n	I	D	n	U	D	Q	I	Н	0	I	D	I	D	D				50	100									
ecies	POTR	LA	LA A	LA		LA L				Y.		TR	-V		LA I									,							
gNo Sp	1 PO	2 ABLA	3 ABLA	4 ABLA	5 ABLA	6 ABLA	7 ABLA	8 PICO	9 POTR	10 ABLA	11 ABLA	12 POTR	13 ABLA	14 POTR	15 ABLA	16 POTR	17 POTR	-	. 5		200					-				-	
	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10		and the same	0000	-34)	-				H	7.0	
Date	6/11/201	6/11/2010	6/11/2010	6111 6/11/2010	6111 6/11/2010	6111 6/11/2010	6111 6/11/2010	6111 6/11/2010	6111 6/11/2010	6111 6/11/2010	6111 6/11/2010	6111 6/11/2010	6111 6/11/2010	6111 6/11/2010	6111 6/11/2010	6111 6/11/2010	6111 6/11/2010						1		18						
PlotID	6111	6111	6111 (111	111	111	111	111	111	111	111	111	111	111	111	114	111		Haz		70										

Fine Woody Debris (< 8 cm) and duff/litter depths 15-m (Pt 1.) and 25-m (Pt. 2) from plot center Pr. 2 10-0.6 cm (0.6-2.5 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 10-0.6 cm (0.6-2.5 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 10-0.6 cm (0.6-2.5 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 10-0.6 cm (0.6-2.5 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 10-0.6 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 Pt. 2 Pt. 1 10-0.6 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 Pt. 2 Pt. 1 10-0.6 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 Pt. 2 Pt. 1 10-0.6 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 Pt. 2 Pt. 1 10-0.6 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 Pt. 2 Pt. 1 10-0.6 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 Pt. 2 Pt. 1 Pt. 2 Pt. 1 10-0.6 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 Pt. 2 Pt. 1 10-0.6 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 Pt. 2 Pt. 1 10-0.6 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 Pt. 2 Pt. 1 10-0.6 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 Pt. 2 Pt. 1 10-0.6 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 Pt. 2 Pt. 1 10-0.6 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 Pt. 2 Pt. 1 Pt. 2 10-0.6 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 Pt. 2 Pt. 1 Pt. 2 10-0.6 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 Pt. 2 Pt. 1 Pt. 2 10-0.6 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 Pt. 2 Pt. 1 Pt. 2 10-0.6 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 Pt. 2 Pt. 1 Pt. 2 10-0.6 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 Pt. 2 Pt. 1 Pt. 2 10-0.6 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt. 1 Pt. 2 Pt. 1 Pt. 2 10-0.6 cm (2.5-8.0 cm Pt. 1 Pt. 2 Pt
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Bearing to plot center	5	10	35	62	85	87	100	110	152	208	239	322																
plot center (m)	4.73	7.06	4.99	7.3	4.13	7.73-	6.46	1.52	2.92	6.17	1.75	2.68		,*														
# years dead		5 years ago: only large twigs remaining													To.							*					47	
Mort	100	n															7											
DecayC	×	3	×	×	×	×	×	×	×	×	×	×		100														
rwthRt	î		î	^	Î	^	î	^	^	î	Î	î							277					100		887		
Age G																											Н	
CrBHt	5.6		0.7		2.1	To the same	0.8	1.3	0.4	6.0	1.5	2.4																
TagNo Species TreeStat DBH Height LICPCI LIC/EHt Age GrwthRt DecayCl Mort	02	0	70	40	80	10	40	40	20	40	20	30																
ght	24		16.1		15.7		16.5	14.6	17.9	20.7	13.2	15.9						,			0							
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s Tree	Ξ	O	I	I	I	n	Ξ	Ι	Ξ	I	Ξ	I				*												
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TagNo	1	2	3	4			7	8	6	10	11	12	1															
Date	7/1/2010	7/1/2010	7/1/2010	7/1/2010	7/1/2010	7/1/2010	7/1/2010	7/1/2010	7/1/2010	7/1/2010	7/1/2010	7/1/2010	7		100													
PlotID				22		22		22	22	22	22	22					7.0				1	1	+					

Coarse Woody Debris (> 8 cm) -- If the central axis of the piece lies in or below Decay Class the duff layer then it should not be Diameter (cm) * note measurements rog # Transect 27 120 Litter depth (cm)
Pt. 1 Pt. 2 Duff/litter measurement Vegetation sampling cylinder 00
 shrub cover
 shrub cover
 Live herb
 Dead herb
 Avg. herb
 Rock cover
 Soil cover

 (%)
 (%)
 cover (%)
 height (m)
 (%)
 (%)
 (%)

 pt. 1
 pt. 2
 35 05 Fine Woody Debris (< 8 cm) and duff/litter depths 15-m (Pt 1.) and 25-m (Pt. 2) from plot center 0 0 Vegetation Cover- 1-m radius plot at 15-m (Pt. 1) and 25-m (Pt. 2) from plot center
Live tree / Dead tree / Shrub cover shrub cover live herb Dead herb Avg. herb Rock cover Litter & duff depth (cm) ~2年い 10 0 Pt. 2 0 Vegetation sampling cylinder Pt. 1 0 Crew lead: 1-hr 10-hr 100-hr 100-hr (0 - 0.6) cm (2.5 - 8.0) cm 00 04 Duff/litter 00 6.5 100-hr 30 0 -0 1512 18/m Date: 5 0 15 Slope (%) 1-0° S 2-120° WP 3-240° S 0-180° S 0-18 Plot ID: Transect 1 - 0° 2 - 120° 3 - 240° 4 - 60° 5 - 180° 6 - 300° O meter 0 feet

